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Classification, Description, and Dynamics of Plant Communities After Fire in the Taiga of Interior Alaska

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Abstract

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One hundred thirty forest stands ranging in age from 1 month postfire to 200 years were sampled and described by successional series (white spruce and black spruce) and by developmental stage (newly burned, moss-herb, tall shrub-sapling, dense tree, hardwood, and spruce). Patterns of change in the two successional series are described. In addition, 12 mature forest communities are described in quantitative and qualitative terms.

Keywords: Communities (plant), classification (plant communities), fire (-plant ecology, taiga, Alaska (interior)).

Summary

One hundred thirty forest stands in the taiga were sampled after fire. They ranged in age from 1 month postfire to 200 years and were located mostly along the road system in interior Alaska south of the Yukon River. Each stand was at least 2 hectares in size, homogeneous in composition, and representative of the surrounding vegetation.

Each area was described in quantitative and qualitative terms, using inventory procedures adapted from Ohmann and Ream (1971). The communities were grouped by site type (white spruce and black spruce) and six developmental stages: (1) newly burned, (2) moss-herb, (3) tall shrub-sapling, (4) dense tree, (5) hardwood (or hardwood-spruce), and (6) spruce. Stands 50–200 years old were aggregated; 12 mature forest community types were then identified and described, using data collected in this study. These are:

1. Populus tremuloides/Viburnum edule/
Linnaea borealis
2. Betula papyrifera/Viburnum edule
3. Betula papyrifera/Alnus crispa/
Calamagrostis canadensis
4. Picea glauca/Viburnum edule/
Equisetum arvense/Hylocomium splendens
5. Picea glauca/Rosa acicularis/ Equisetum
sylvaticum/Hylocomium splendens
6. Populus balsamifera/Oplopanax horridus

7. Populus tremuloides-Picea mariana/
Cornus canadensis

8. Picea mariana-Betula papyrifera/
Vaccinium uliginosum-Ledum groenlandicum

9. Picea mariana/Vaccinium uliginosum-
Ledum groenlandicum/Pleurozium schreberi

10. Picea mariana/feathermoss-lichen

11. Picea mariana-P. glauca/Betula
glandulosa/lichen

12. Picea mariana/Sphagnum spp.-Cladina spp.

The community types are named by their dominant species. Slashes separate vegetation strata—trees, tall shrub, low shrub, and/or forest floor. Hyphens between plant names indicate codominance within a strata. Types 1–4 occur on upland white spruce sites, types 5 and 6 on bottomland white spruce sites, types 7–10 on mesic black spruce sites, type 11 near timberline, and type 12 on moist black spruce sites. This list is not exhaustive. Other forest community types exist but were not encountered in this study. The mature vegetation community types described are included in a vegetation classification system proposed for Alaska (Vioreck and Dyrness 1980).

Succession is described separately for white spruce and black spruce sites, using data obtained in this study, first statistically by developmental stage, then dynamically by patterns of change that span all stages of both successional series. The successional series are also compared.

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Introduction

Wildfire is an integral part of the taiga in Alaska. Wildfires caused by lightning or human activities burn 1.4 thousand to 2 million ha each year^{1/} (Barney 1971b). Reoccurring fires encourage fire resistant species such as black spruce^{2/} and fast growing species such as quaking aspen and paper birch (Lutz 1956).

Since the 1950's, people have attempted to prevent wildfires and reduce the acreage burned. Fire suppression activities may protect houses, towns, and important resources like commercial timber; however, they may also scar the landscape, encourage erosion, and set back vegetation development even more than fire itself. Poorly designed and placed firelines can increase gully erosion, surface subsidence, and stream siltation. This is especially true if large vehicles are used in areas of ice-rich permafrost (DeLeonardis 1971, Lotspeich and Mueller 1971).

Furthermore, if all fires were controlled, other problems would occur. The landscape would become less diverse. Young stands of trees would be rare. Quaking aspen or white spruce would occur on the very warm and well-drained sites, whereas black spruce and bog would occur elsewhere. Paper birch would be less plentiful, and balsam poplar would grow only on flood plains adjacent to rivers (Neiland and Viereck 1977, Viereck 1973). Animals that are dependent on any stages of succession except the oldest would become rare or disappear, and predators of these animals would become rare or move elsewhere.

^{1/}Fire data on file at the State Office, Bureau of Land Management, U.S. Department of the Interior, Anchorage, Alaska.

^{2/}Scientific names for species are given in the appendix.

Fire has many uses. Aboriginal man used it for warmth, cooking, hunting, signaling, and insect control (Lutz 1959). Homesteaders and miners use it to clear land and thaw frozen ground. Fire can be used in Alaska to regulate fuel accumulation on the forest floor, to dispose of timber harvest slash, and to manipulate wildlife habitat. It can also be used to help prepare seedbeds for regeneration or to convert a stand from one species to another. Personnel on the Chugach National Forest and the Kenai National Moose Range currently use controlled fire to manipulate moose habitat.

Many land managers are actively seeking information on fire effects and the potential use of controlled fire. Interest in and concern for quality land management is high and increasing because of changing patterns of land ownership. Whether land managers are preserving natural vegetation or manipulating it for special uses, they must define the role fire will play in their management plans.

Understanding the effects of fire in Alaska began with the work of Harold Lutz in the early 1950's (Lutz 1956) and has evolved in a slow, discontinuous manner. In 1971, the Alaska Forest Fire Council and the Society of American Foresters sponsored a symposium, "Fire in the northern environment" (Slaughter and others 1971), which summarized the current status of research and management related to fire in Alaska and parts of northern Canada. Viereck (1973) reviewed most of the current and early work on fire effects in the taiga of Alaska and northwest Canada. Kelsall and others (1977) and Viereck and Schandelmeier (1980) expanded and updated the review by Viereck. The interested reader can refer to these papers for a more detailed discussion of fire effects in Alaska.

Objectives

Field studies on the effects of fire began at the Institute of Northern Forestry in 1971 with a series of studies designed to document the immediate and long-term effects of the 1971 Wickersham fire on forest ecosystems. A series of experimental fires in 1976 and again in 1978 adjacent to the Wickersham fire area were analyzed to provide information on fire behavior as well as prefire and immediate postfire data. Two papers (Viereck and Dyrness 1979, and Viereck and others 1979) summarize work undertaken in and around the area of the Wickersham fire from 1971 to 1976. Additional work on postfire seed germination and revegetation (Claudice 1974), on small mammals (West 1977, 1979) and on moose and snowshoe hare browse (Wolff 1977, 1978) was also done in this study area.

This paper reports the first phase of some research that began in the Wickersham fire area and expanded to other areas in the Alaska interior. The project was funded by the U.S. Department of the Interior, Bureau of Land Management; National Science Foundation; and USDA Forest Service.

This study has two objectives: to qualitatively and quantitatively describe plant communities or forest types in the taiga, and to order these community types into successional patterns for white spruce and black spruce sites.

The study is being undertaken in three phases. Phase I, reported here, focuses on the classification of the different communities found and the description of the community types.^{3/4/} It does not describe or statistically predict the composition of each type. Phases 2 and 3 will increase both the number of community types and the number of replications studied.

^{3/} A community is real in the landscape. A community type is theoretical.

^{4/} This paper is an expansion of a portion of the following report. Foote, M. Joan. Classification, description and dynamics of plant communities following fire in the taiga of interior Alaska. Final report for the Bureau of Land Management, 211 p., 1976. On file at the Institute of Northern Forestry, Fairbanks, Alaska.

The Study Area

Taiga, or northern boreal forest, covers 43 million ha (Viereck 1973) to 60 million ha^{5/} in Alaska. It is bounded on the north by the Brooks Range, on the west by maritime tundra, on the south by maritime forest, and on the east by the Canadian taiga. Within this area, forests are bounded at higher elevations by alpine tundra, ice, and snow and at lower elevations by lakes and muskeg.

The study area of phase I consisted of linear strips 5–10 km wide along the road system in interior Alaska south of the Yukon River and a few remote locations elsewhere where aerial access was provided. Most of the study area was in the western portion of the Tanana River valley and adjacent highlands (fig. 1). Phases 2 and 3 of the study will expand the area to the road system north of the Yukon River, to the Tanana River flood plain southwest of Fairbanks, and to more remote portions of the taiga.

The climate of the taiga is continental and characterized by extreme temperatures, low precipitation and light surface winds (Searby 1968). Variations over short distances are considerable, and departures from the mean are common. U.S. Weather Bureau records for Fairbanks typify the climate of the study area. The average annual temperature is -3.5°C ; extremes are -51° and 38°C . The mean maximum and minimum temperatures for summer are 22° and 3.8°C and for winter are -2.7° and -30°C , respectively. The average annual total precipitation is 28 cm. The annual snowfall averages 178 cm and remains from mid-October to mid-May. Solar input averages 531 langleys in June and 6 langleys in December; the former reflects the 24-hour-long sunlit days of summer whereas the latter reflects the short, 8-hour sunlit periods in winter. The

frost-free growing season lasts from mid-June to early August. The total growing season, based on a degree day of 4.4°C , is about 1,900 hours long (Selkregg 1976, p. 43–44). The cumulative sum of daily mean temperatures for the growing season, using a degree day base of 6°C , is 940°C (Funsch 1964).^{6/}

The taiga of Alaska, according to Thornthwaite's (1931) evapotranspiration classification system, has a potential evapotranspiration of 356–457 mm, and the climate can be described as semiarid, with little or no surplus rainfall and with temperature efficiency normal to warm microthermal (Patric and Black 1968). Trigg (1971), using index values of effective precipitation and temperature, categorized interior Alaska as hot-arid to warm-dry, or as an area of high fire frequency.

The geology of interior Alaska varies from Precambrian rocks to Pleistocene loess. Bedrock in the Fairbanks Hills, including the area around Fairbanks and Wickersham Dome, is weathered Precambrian micaceous schist of the Birch Creek formation (Viereck and Dyrness 1979) under a layer of Pleistocene loess. To the north and east of the Fairbanks Hills the bedrock is a mixture of metamorphic, sedimentary, and volcanic rocks of Paleozoic age (Wahrhaftig 1965). The loess layer varies from 0 cm on the hilltops to over 60 m around Fairbanks (Péwé 1968). Some loess has been washed down from the hills to the valley bottoms where it forms deposits of bedded to massive silt rich in organic debris (Péwé 1975).

^{6/} A degree day, used to describe the growing season more precisely, is a day when the mean temperature is above a certain threshold (Selkregg used 4.4°C ; Funsch, 6°C).

^{5/} Joint Federal-State Land Use Planning Commission for Alaska. Ecosystem area figures computed for the 1980 Renewable Resources Planning Act field effort, 1976. On file at the Institute of Northern Forestry, Fairbanks, Alaska.

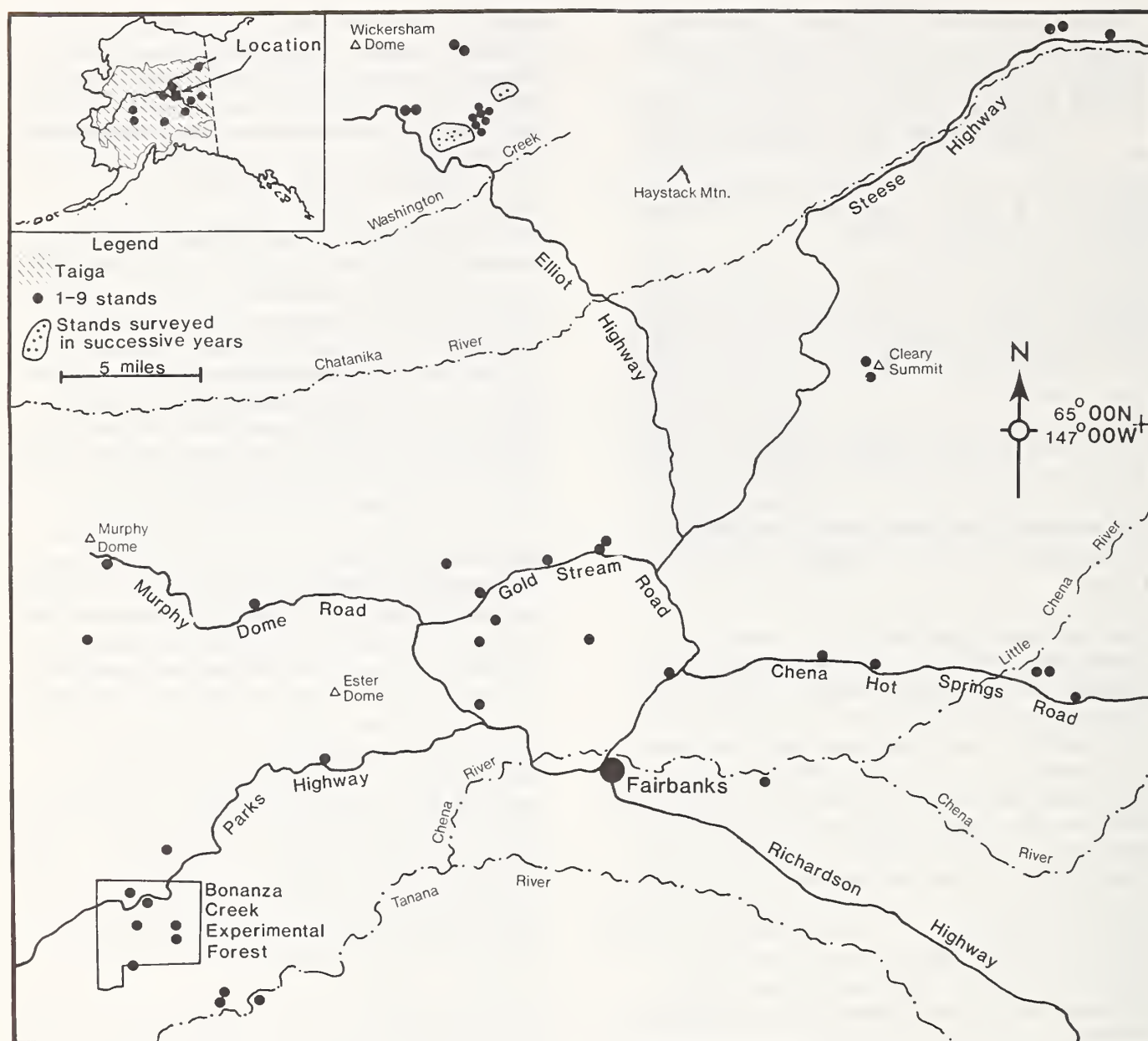


Figure 1.—Location of study areas in the Alaskan taiga.

Soils of the taiga tend to be poorly developed Inceptisols, undeveloped Entisols, or Histosols (Rieger and others 1979). Ochrepts or well-drained Inceptisols (soils that have only small amounts of organic material in the upper few centimeters) occur on hills where permafrost is nonexistent or deep. Wet Inceptisols or Aquepts (soils with thin to thick layers of mostly undecomposed organic material) occur in poorly drained areas where ice-rich permafrost is shallow to deep. Flood plains, outwash plains, and seepage areas may have exposed wet mineral soils or Entisols. These are mostly Aquepts or Fluvents, depending on whether the water table is shallow or deep. Histosol soils, like Fibristis, are deep organic soils mostly of undecomposed sphagnum or peat. These occur in depressions or in moist areas of long standing. Permafrost may or may not be present, but ice does remain until late in the growing season.

Permafrost is common on north-facing slopes or valley bottoms which receive little solar radiation (Brown and Péwé 1973). This frozen layer underlies an active soil layer which freezes and thaws each year during the warm period. Permafrost influences plant growth because it impedes the downward penetration of roots and keeps the active soil layer cool. This, in turn, slows down litter decomposition and cell growth. The frozen layer also prevents percolation; accumulated water may counteract the effect of low rainfall and enhance growth or, as in most areas, impede tree growth and result in the development of muskeg, bogs, and ponds.

Topography, ground surfaces, and plant cover are potential interceptors of solar radiation. Hills, soils high in silts, clays or peat, moss mats, and tree canopies tend to decrease the effect of incoming solar radiation. Thus soils on north-facing slopes, soils under moss mats or dense vegetation canopies, and soils which are high in silts, clays, or peat are usually cool and underlain by permafrost. South slopes, coarse-grained sediments, bare rock surfaces, moss-free surfaces, and treeless surfaces which absorb incoming solar radiation tend to be warmer and free of permafrost (Selkregg 1976, p. 100).

Fires, both natural and human caused, can occur in interior Alaska between April 1 and September 30, but most occur in May, June, or July. Probability indexes of fire occurrence (buildup index) reach peak values from June to early July (Barney 1967). This is when temperatures are highest, nighttime cooling is minimal, humidities are lowest, there are long periods with little or no precipitation, and lightning storms are frequent.

Fires burn extensive area each year. Before fire suppression—1893 to 1939—Lutz (1953) estimated 405 000 ha burned annually. Barney's (1971 a, b) more recent estimate is 0.6–1.0 million ha per year. For the time of active fire suppression—1940 to 1979—the area burned averaged 201 700 to 502 400 ha per year, based on 10-year intervals (table 1). Two trends are apparent from the data in table 1: the total area burned each year is decreasing, and the total number of fires reported has increased each decade. These trends probably reflect improvements in fire control and detection.

Table 1—Number of fires and area burned per year in interior Alaska, 1940-79

Number of fires and area burned per year	1940-49		1950-59		1960-69		1970-79	
	Amount	Percent	Amount	Percent	Amount	Percent	Amount	Percent
	<u>Number</u>		<u>Number</u>		<u>Number</u>		<u>Number</u>	
Fires per year:								
Human caused	93.8	82	183.9	71	152.7	64	130.2	42
Lightning caused	20.0	18	74.5	29	85.3	36	180.5	58
Total fires	113.8	100	258.4	100	238.0	100	310.7	100
	<u>Thousand hectares</u>		<u>Thousand hectares</u>		<u>Thousand hectares</u>		<u>Thousand hectares</u>	
Area burned per year:								
Human caused	—	—	88.4	20	63.3	25	3.8	2
Lightning caused	—	—	344.2	80	194.4	75	197.9	98
Total area burned	502.4	100	432.6	100	257.7	100	201.7	100

— = No data.

Sources: (a) Fire data on file at the State Office, Bureau of Land Management, U.S. Department of the Interior, Anchorage, Alaska. (b) Barney (1971b).

Fires in interior Alaska occur primarily on tundra, bog, and noncommercial forest lands (Viereck 1973). Barney (1971a) and Viereck (1975) give the following breakdown by cover type, based on 5 years of data: treeless (includes tundra, bog, and grassland) 43 percent; conifer forest (primarily black spruce) 36 percent; conifer-broadleaf forest 14 percent; broadleaf (aspen, birch, and cottonwood) 2 percent; and other (high brush) 5 percent. Barney (1971a) further states that less than 0.5 percent of the burned forested land could be classified as potential commercial forest land or land capable of producing 1.4 m³ of wood per hectare per year.

Human impact on the forests has varied and early impacts have been masked by those which came later. Trees are harvested mostly for local timber and fuel needs as the land is cleared for settlements, roads, power transmission lines, pipelines, and farms. Fires are associated with these activities. The presence of numerous 50- and 80-year-old forest stands reflects increases in human activities during the early 1900's and the mid-1920's.

Methods

Stands were selected to represent variations in (1) mature forest community type, (2) stage of forest development, and (3) range of fire effects. Stands considered for selection were limited to those that were homogeneous in nature, at least 2 ha in area, and representative of the surrounding vegetation and topography. Eighteen burns of known age and numerous burns of unknown age were visited. The burns of known age dated from the following fires: Porcupine (1950), Badger Road (1958), Chena Dome (1958), Healy (1958), Chena Hot Springs Road (1957–58), Murphy Dome (1958), Goodpaster (1958), Standard (1966), Harding Lake (1966), Hess Creek (1966), Cement Creek (1966), Steese–Chena Hot Springs Road Junction (1968), Manley (1969), Wickersham (1971), Ganes Creek (1971), Nixon Flats (1971), Grenac Road (1977), and Parks Highway (1977). Some burned stands were revisited annually or intermittently to monitor vegetation development.

Each stand selected was studied using a grid of usually 20 points that were approximately 20 m apart and organized along the long axis of the stand. At each point a nest of three plots was used to collect: (1) visual estimates of canopy cover, (2) stem counts by diameter class, (3) seedling counts, (4) tree d.b.h. (diameter at breast height), and (5) distance to plot center. A 1-m² plot was used to estimate cover for cryptogams, herbs, low shrubs, exposed ground surface, and litter categories. A 4-m² plot was used to estimate cover, and to count stems for tall shrubs and seedling trees (Ohmann and Ream 1971); and a point-centered quarter plotless method (Cottam and Curtis 1956) was used to count and measure live sapling, live adult, and standing dead trees. Depths of litter, organic soil, and depth to permafrost were measured adjacent to but outside the 1-m² plots. Each permafrost measurement was dated. In addition, 15 trees were bored, fire-scarred trees were sectioned, and 2–5 photos were taken of both the general stand and the small 1-m² plots.

The following data were then summarized for each stand: (1) mean percent cover for all plant species, ground surface and litter categories, and vegetation layers (moss, lichen, herb, low shrub, tall shrub, and tree), (2) average density per hectare for tree seedling, tree, and tall shrub species, (3) average basal area per hectare for each tree species, (4) average d.b.h. for trees and saplings, (5) distribution of trees and saplings by 1-cm d.b.h. classes, (6) stand age based on annual ring counts, (7) thickness of the surface organic layer, (8) depth to permafrost and date, and (9) mean frequency of plant species encountered in sample plots. Stand photographs were labeled and filed.

Similar stands were identified and grouped with the aid of a computerized clustering system. The technique used in the system is a polythetic agglomerative numerical classification which, based on within-group dispersion using standard distance, pairs most similar stands or stand-groups in successive cycles to produce a hierarchy of stand relationships (Orloci 1967). The number of stand groups recognized from this technique depends on the level of hierarchy that is found to be meaningful. For this study, stand groupings were used if they subjectively represented: (1) previously defined plant community types (Lutz 1956, Viereck 1973), (2) tentatively defined plant community types (Viereck and Dyrness 1980), or (3) were visually discrete units of the landscape but not previously identified.

The clustering program required use of a reduced species list (see appendix). To make the selection as objective and quantitative as possible, the computer program SCREEN was employed (Grigal and Ohmann 1975). SCREEN ranks the species in the data set on six different criteria: (1) frequency, with those species found in the most plots ranking highest, (2) arithmetic mean of the frequency of each species over all stands, (3) the ratio between

Results and Discussion

the computed standard deviation of observations for each species and the one predicted on the basis of the mean, (4) information based on data recording presence and absence, (5) the relative contributions made by each species in the calculation of interstand distance, and (6) the absolute weighting of each species along the first five principal component axes. This last step results in a ranked list of species. The 59 species to be used in subsequent analyses were selected from those ranking highest on this list, with one exception. In an effort to have each vegetational stratum well represented, some species which fell in the middle of the master lists but high when only their own stratum was considered were included in the reduced species list.

The resulting stand groupings are the community or forest types described in this paper. These types, called community types throughout this paper, represent actual small segments of the taiga landscape. They cannot, in a statistical sense, predict what would occur throughout the entire taiga. They can, however, give a first approximation of the species composition one would expect to find in each of the community types studied.

Additional community types exist. Some are reported in the literature (Neiland and Viereck 1977, Viereck and Dyrness 1980), others have yet to be defined and described.

Taxonomy follows Viereck and Little (1972) for woody plants, Hultén (1968) for herbaceous plants, Worley and Watuski (1970) for mosses, and Hale and Culberson (1970) for lichens. Common names for plant species follow Viereck and Little (1972), Hultén (1968), Kelsey and Dayton (1942), and Welsh (1974). Difficult identifications of species were determined by Alan Batten, David Murray, and Barbara Murray of the University of Alaska herbarium. Voucher plant specimens were collected and were deposited in the University of Alaska herbarium.

One hundred thirty stands, ranging in age from 1 month postfire to 200 years, were located and sampled (see fig. 1). Forty-seven older ones (50–200 years old) were aggregated into most-similar groupings. Twelve of these groups appeared to reflect well-developed, mature communities and were the basis of the mature community types described in this paper (table 2). The 12 groups also appeared to reflect two site types that formed the basis of the developmental stages described later in this paper.

Table 2—Some mature forest community types in the taiga of interior Alaska

Type number	Name of mature forest community type
1	<u>Populus tremuloides/Viburnum edule/</u> <u>Linnaea borealis</u>
2	<u>Betula papyrifera/Viburnum edule</u>
3	<u>Betula papyrifera/Alnus crispa/</u> <u>Calamagrostis canadensis</u>
4	<u>Picea glauca/Viburnum edule/</u> <u>Equisetum arvense/Hylocomium</u> <u>splendens</u>
5	<u>Picea glauca/Rosa acicularis/</u> <u>Equisetum sylvaticum/Hylocomium</u> <u>splendens</u>
6	<u>Populus balsamifera/Oplopanax</u> <u>horridus</u>
7	<u>Populus tremuloides-Picea mariana/</u> <u>Cornus canadensis</u>
8	<u>Picea mariana-Betula papyrifera/</u> <u>Vaccinium uliginosum-Ledum</u> <u>groenlandicum</u>
9	<u>Picea mariana/Vaccinium uliginosum-</u> <u>Ledum groenlandicum/Pleurozium</u> <u>schreberi</u>
10	<u>Picea mariana/feathermoss-lichen</u>
11	<u>Picea mariana-Picea glauca/Betula</u> <u>glandulosa/lichen</u>
12	<u>Picea mariana/Sphagnum spp.-</u> <u>Cladina spp.</u>

Figure 2 portrays the general relationship between stands, stand groups, community types, and site types.

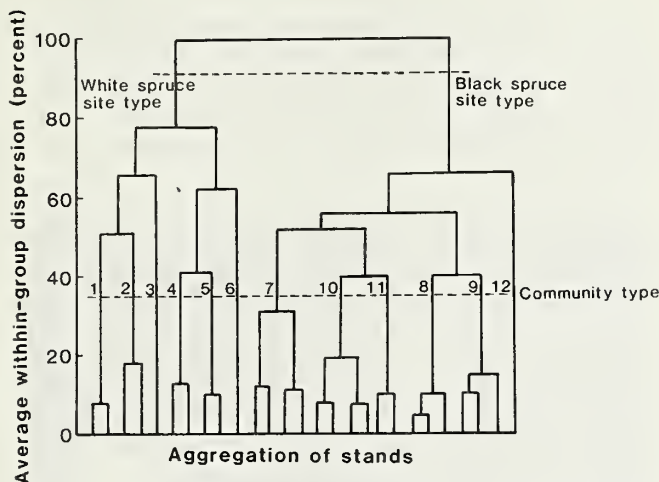


Figure 2.—Stylized dendrogram of stands, stand groups, mature community types, and site types. Vertical lines depict individual stands or groups of similar stands. Connecting horizontal lines indicate the degree of similarity of stands or stand groups; the lower the within-group dispersion, the more similar the stands or stand groups. The lower dashed line identifies the 12 stand groups used to form the 12 mature community types. The upper dashed line identifies the two stand clusters denoting the two site types.

Many taxa were found in all community types. Differences were in amounts of cover, frequency, and density rather than distinct changes in species composition. A mature forest community type gets its name from the plant species which best describes it. Species

that occur in different strata are separated by slashes; species that share the same stratum are separated by hyphens. For example, in the *Picea mariana*-*Picea glauca*/*Betula glandulosa*/lichen community type (table 2, type 11), *P. mariana* and *P. glauca* share dominance in the tree stratum, *B. glandulosa* dominates the tall shrub stratum, and lichens are important on the forest floor.

The revegetation process is continuous. In this study, however, it is divided into six stages representing developmental phases in plant succession. This paper discusses each stage in terms of its place in secondary succession on white spruce or mesic black spruce sites. Each stage is named by its dominant vegetation; age limits are suggested.

Mature Forest Communities

A mature forest community is the most stable phase of development attained by a tree species. It may be, but is not always, synonymous with the end of succession. As defined in this work, maturity occurs when the stand is dominated by trees and the species complex has more or less stabilized. The mature character of a forest community is first apparent when the trees are at least 50 years old. Changes that occur thereafter reflect the age and maturation of individual plants; i.e., trees age, grow larger in diameter, and die. Some mature forest communities are relatively self-perpetuating; others convert to other forest types. In interior Alaska most communities are terminated by fire. The oldest stands are limited to isolated locations or those protected from fire by topography or wetness. For example, river islands are isolated, and bogs and sphagnum-rich, north-facing slopes are usually too wet to sustain fire. But even in such protected locations, no trees older than 300 years have been discovered.

White Spruce Sites

White spruce sites occur on flood plains and river terraces along river margins, on slopes with southern exposures within 8 km of the major river valleys, or near timberline. These sites are generally warm and covered with well-drained Inceptisols and Entisols. Seasonal frost in the soil begins melting in May and is mostly gone by late June. Permafrost is rare and, when present, seldom within 10 m of the surface.

The vegetation is dominated by trees, but tall shrubs, herbs, and sometimes moss are also prominent. Quaking aspen, paper birch, balsam poplar, white spruce, prickly rose, high bushcranberry, field horsetail, and sometimes the feathermoss Hylocomium splendens grow well on white spruce sites. The trees occur in both pure and mixed stands and with the other vegetation produce the community or forest types that occur on white spruce sites. Six of these forest types will be discussed (table 2, types 1-6). Of the six, four (types 1-4) are found on upland slopes and two (types 5-6) are found on flood plains near rivers. Other community types exist on white spruce sites but have not yet been described quantitatively.

1. Populus tremuloides/Viburnum edule/ Linnaea boreale community type

Mature stands of this type are characterized by a closed canopy of quaking aspen (Populus tremuloides) trees, an almost continuous tall shrub layer of prickly rose and high bushcranberry (Viburnum edule), and twin-flower (Linnaea borealis) on the forest floor (fig. 3).



Figure 3.—A Populus tremuloides/Viburnum edule/Linnaea borealis community. Quaking aspen in this stand (no. 259) are 70 years old.

Quaking aspen grows on south-facing slopes up to an elevation of 610 m (Gregory and Haack 1965). These slopes vary in grade between 7 and 40 percent and are covered by a 5- to 10-cm surface horizon of organic material that overlies a mantle of loess 0.1-70 m deep. Quaking aspen trees grow on the warmest forest sites in interior Alaska. Snow melts early in the spring. The seasonal frost retreats to a minimum depth of 80 cm by late June and is entirely gone by August. Soils on these sites can become extremely dry. Wherever quaking aspen occurs, Populus tremuloides/Viburnum edule/Linnaea boreale communities may also occur.

This study found the flora in communities of this type to be moderately diverse; each stand studied possessed 30-38 plant species. Species with frequencies averaging 40 percent or more (that is, species occurring on 40 percent or more of the sample plots) are listed in table 3. No species is unique to this community type. Species such as quaking aspen, high bushcranberry, twin-flower, and Labrador lousewort, however, appear to prefer these warm, well-drained forest sites. Bebb willow, which occurs widely in seral communities, remains a component of only this community type, and even here it is not common.

Communities of this type are mature when the quaking aspen reach 50-80 years of age. At that time the tree canopy is continuous. Data from this study show that tree densities average 1,200 trees/ha, diameters range from 3- to 35-cm d.b.h. but average 17 cm, and heights range from 17 to 26 m. Paper birch, white spruce, and balsam poplar also occur but are infrequent. In overmature stands 130 years old, the canopy is open, tree density has decreased to 700 trees/ha, and diameters increased to more than 40-cm d.b.h. and average 32.8 cm.

Prickly rose and high bushcranberry form an almost continuous tall shrub layer 1-1.5 m tall in both mature and overmature stands. Mean frequencies for both species range between 85 and 100 percent. Two additional tall shrubs, American green alder and Bebb willow, occur occasionally or at frequencies of less than 30 percent.

The low shrub layer is composed of patches of twin-flower and sometimes mountain-cranberry. The former, with a mean frequency of 65 percent, is common; the latter, with a frequency of 0-40 percent, is occasional.

The herb layer is composed of scattered plants. It is dominated by field horsetail, bunchberry, and fireweed. Reedgrass is only slightly less important. The following species were present in most of the stands studied: tall bluebell, one-sided wintergreen, liverleaf wintergreen, bluntleaved sandwort, Geocaulon lividum, and northern bedstraw. Herbs tend to be less common and less extensive in the overmature stands; however, this may not be so with northern bedstraw, Geocaulon lividum, and bluntleaved sandwort.

Mosses, when present, grow on the basal trunks and exposed roots of quaking aspen or occasionally in small patches on the forest floor. Lichens, primarily Cladonia spp., occur but never in large amounts. Leaf litter covers most of the forest floor to a depth of 1-2 cm.

Table 3—Important plant species and litter components of the Populus tremuloides/Viburnum edule/Linnaea borealis community type (Type 1) of interior Alaska

Species and litter component	Mature stands 1/				Overmature stands 6/			
	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/
	Percent	Stems/ha	Cm	Percent	Percent	Stems/ha	Cm	Percent
Tree layer:								
<u>Populus tremuloides</u> —								
Mature trees	—	1,200	15–19	100	—	700	32.8	100
Saplings	—	0	—	0	—	500	—	100
Seedlings	—	1,700	—	16	—	8,800	—	50
Tall shrub layer:								
<u>Rosa acicularis</u>	—	30,000	—	92	—	28,000	—	100
<u>Viburnum edule</u>	—	40,000	—	87	—	213,000	—	100
Low shrub layer:								
<u>Linnaea borealis</u>	9	—	—	65	3	—	—	90
Herb layer:								
<u>Calamagrostis</u> spp.	1	—	—	78	0	—	—	0
<u>Cornus canadensis</u>	9	—	—	90	7/	—	—	20
<u>Epilobium angustifolium</u>	3	—	—	85	3	—	—	60
<u>Equisetum arvense</u>	10	—	—	78	0	—	—	0
<u>Galium boreale</u>	7/	—	—	23	2	—	—	70
<u>Geocaulon lividum</u>	7/	—	—	7	4	—	—	40
<u>Moehringia lateriflora</u>	7/	—	—	20	1	—	—	50
Litter component:								
Leaves and twigs	93	—	—	100	94	—	—	100
Dead wood and fallen logs	6	—	—	93	11	—	—	100

- 1/ Number of mature stands sampled: 3; age: 50-70 years; number of species found: 31-38; depth of organic layer: 10 cm.
- 2/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: $\text{Cover} = \frac{\Sigma (\text{mean stand cover value for a species})}{\text{total number of stands sampled}}$. The values given are rounded to the nearest whole number.
- 3/ The computed or counted number of stems occurring in a given area. It is based on the equation: $\text{Density} = \frac{\Sigma (\text{mean stand density value for a species})}{\text{total number of stands sampled}}$. The values given above 200 are rounded to the nearest 100; the values below 100 are rounded to the nearest whole number.
- 4/ D.b.h. is the diameter of a tree at breast height. The mean stand d.b.h. value for a species is given; when more than 1 stand was sampled, the range of mean values is given.
- 5/ The percent of plots in which a given species occurs. It is based on the equation: $\text{Frequency} = \frac{\Sigma (\text{mean stand frequency value for a species})}{\text{total number of stands sampled}}$. The values given are rounded to the nearest whole number.
- 6/ Number of overmature stands sampled: 1; age: 130 years; number of species found: 22; depth of organic layer: 8 cm.
- 7/ Less than 0.5 percent.

Stands in this community type may be able to maintain themselves through several generations because young aspen frequently outnumber young stems of other species. Occasionally local patches of dense paper birch seedlings develop, but there is no evidence that these survive for long. White spruce eventually invades, and if no fire occurs, this quaking aspen community will evolve into a white spruce community. If fire occurs, quaking aspen will probably replace itself.

The Populus tremuloides/Viburnum edule/Linnaea borealis community type is one of several quaking aspen types. This type and the closed Populus tremuloides/Viburnum edule/Linnaea borealis type (Viereck and Dyrness 1980) are based on the aspen/Viburnum/twin-flower type of Foote (see footnote 4). It is a component of the more general aspen type (Buckley and Libby 1957, Hutchison 1968, Lutz 1956, Neiland and Viereck 1977, and Viereck and Little 1972). On vegetation maps with scales of 1:2,500,000 and 1:7,500,000, it is included in the upland spruce-hardwood forest type (Joint Federal-State Land Use Planning Commission for Alaska 1973), the spruce-birch forest type (Küchler 1966), and the moderately high, mixed evergreen and deciduous forest type (Spetzman 1963). Other aspen types are discussed in Neiland and Viereck (1977) and Viereck and Dyrness (1980).

2. Betula papyrifera/Viburnum edule community type

Mature stands of this type are characterized by dominance of paper birch (Betula papyrifera) trees, an extensive tall shrub layer of prickly rose and high bushcranberry (Viburnum edule), and an open herb layer of field horse-tail (fig. 4).



Figure 4.—A Betula papyrifera/Viburnum edule community. Paper birch in this stand (no. 122) are 60 years old.

Paper birch grows on east- and west-facing slopes at elevations below 610 m. Slopes vary in grade between 7 and 40 percent and have a 10- to 15-cm surface horizon of organic material on top of loess.

Sites supporting paper birch are not as warm as those supporting quaking aspen. In the paper birch stands snow stays until early May, and the seasonal frost leaves more slowly. In late June the ground thaws to a minimum depth of only 50 cm; however, by August the frost layer is gone.

The flora of this community type was found to be sparse; the stands studied averaged 23-28 species—considerably fewer than the number found in the Populus tremuloides/Viburnum edule/Linnaea borealis community type. Species with mean frequencies of 40 percent or more are listed in table 4.

Table 4—Important plant species and litter components of the Betula papyrifera/Viburnum edule community type (Type 2) of interior Alaska

Species and litter component	Mature stands 1/				Overmature stands 6/			
	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/
	Percent	Stems/ha	Cm	Percent	Percent	Stems/ha	Cm	Percent
Tree layer:								
<u>Betula papyrifera</u> —								
Mature trees	—	800	20.8–21.2	100	—	200	32.3	100
Saplings	—	5	—	8	—	7	—	50
<u>Picea glauca</u> —								
Mature trees	—	100	13.9–15.5	30	—	40	41.4	50
Saplings	—	5	—	5	—	10	—	65
Tall shrub layer:								
<u>Rosa acicularis</u>	—	15,000	—	85	—	13,000	—	100
<u>Viburnum edule</u>	—	12,000	—	50	—	18,000	—	55
Low shrub layer:								
<u>Linnaea borealis</u>	1	—	—	40	7/	—	—	35
Herb layer:								
<u>Calamagrostis</u> spp.	7/	—	—	2	3	—	—	75
<u>Cornus canadensis</u>	2	—	—	75	1	—	—	60
<u>Epilobium angustifolium</u>	2	—	—	35	2	—	—	55
<u>Equisetum arvense</u>	31	—	—	80	17	—	—	95
Moss:								
<u>Pleurozium schreberi</u>	1	—	—	20	3	—	—	40
Litter component:								
Leaves and twigs	93	—	—	100	90	—	—	100
Dead wood and fallen logs	4	—	—	55	6	—	—	65

- 1/ Number of mature stands sampled: 2; age: 60-100 years; number of species found: 23; depth of organic layer: 13 cm.
- 2/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: $\text{Cover} = \frac{\Sigma (\text{mean stand cover value for a species})}{\text{total number of stands sampled}}$. The values given are rounded to the nearest whole number.
- 3/ The computed or counted number of stems occurring in a given area. It is based on the equation: $\text{Density} = \frac{\Sigma (\text{mean stand density value for a species})}{\text{total number of stands sampled}}$. The values given above 200 are rounded to the nearest 100; the values below 100 are rounded to the nearest whole number.
- 4/ D.b.h. is the diameter of a tree at breast height. The mean stand d.b.h. value for a species is given; when more than 1 stand was sampled, the range of mean values is given.
- 5/ The percent of plots in which a given species occurs. It is based on the equation: $\text{Frequency} = \frac{\Sigma (\text{mean stand frequency value for a species})}{\text{total number of stands sampled}}$. The values given are rounded to the nearest whole number.
- 6/ Number of overmature stands sampled: 1; age: 140 years; number of species found: 28; depth of organic layer: 13 cm.
- 7/ Less than 0.5 percent.

Stands of the Betula papyrifera/Viburnum edule communities are mature when the paper birch reach 60–90 years of age. At that time the tree canopy is closed. Tree densities average about 800 stems/ha, diameters range from 2.5 to 48-cm d.b.h. but average 21 cm, and heights range from 12 to 24 m. In overmature stands, which are common, the mean tree density has decreased to 200 stems/ha, and diameters of the larger trees range from 15.7- to 68.3-cm d.b.h. Gregory and Haack (1965) found that trees more than 40-cm d.b.h. are usually defective. White spruce trees occur but in fewer numbers. Saplings of both white spruce and paper birch may occur in small numbers; seedlings are rare.

A tall shrub layer reaches 1–1.5 m in height, and a shorter herb layer occurs beneath the trees. Prickly rose is ubiquitous, high bush-cranberry is common, and clumps of American green alder occur occasionally. Field horsetail and leaf litter dominate the forest floor. Scattered throughout the stands are other herb species such as bunchberry, bluntleafed sandwort, reedgrass, and fireweed; low shrub species such as twin-flower; and feathermoss species such as Pleurozium schreberi and Hypnum splendens. The amount of reedgrass and Pleurozium schreberi increases with stand age. Leaf litter forms a continuous layer 2–3 cm thick. Occasional rotting logs and short hollow snags, mostly of paper birch, are found on the forest floor.

This community type appears to be composed of even-aged stands. The white spruce and paper birch most likely started from seed before heavy leaf litter developed. Gregory (1966) found that heavy leaf litter falling in mature paper birch stands prevents the establishment and survival of young white spruce seedlings. Regeneration of paper birch within mature stands is mostly limited to stem suckers, which sometimes ring the base of old trees. Eventually, however, the slower growing white spruce will replace the defective overmature paper birch in the tree canopy, and the community will succeed to an open white spruce type.

The Betula papyrifera/Viburnum edule community type and the closed type of the same name (Viereck and Dyrness 1980) are based on the birch/Viburnum type of Foote (see footnote 4). The open Betula papyrifera/Viburnum edule/Calamagrostis type (Viereck and Dyrness 1980) may be closely related. In any case, it is a component of the more general birch, paper birch, or white birch types (Buckley and Libby 1957, Hutchison 1968, Lutz 1956, Neiland and Viereck 1977, and Viereck and Little 1972). On vegetation maps with scales of 1:2,500,000 and 1:7,500,000, it is one component of the even more generalized types: upland spruce-hardwood forest (Joint Federal-State Land Use Planning Commission for Alaska 1973), spruce-birch forest (Küchler 1966), and moderately high, mixed evergreen and deciduous forest (Spetzman 1963). Additional paper birch types are discussed by Neiland and Viereck (1977) and Viereck and Dyrness (1980).

3. Betula papyrifera/Alnus crispa/Calamagrostis canadensis community type

Mature stands of this type are characterized by a closed canopy of paper birch (Betula papyrifera) trees and extensive patches of tall American green alder (Alnus crispa) (fig. 5).

Stands typifying this community type occur on east- and west-facing slopes below 610 m. Slopes vary in grade between 10 and 30 percent, and a 10- to 15-cm surface horizon of organic material overlies a thin mantle of loess. Soil temperatures appear to be cooler than on the south-facing slopes—at least the seasonal frost retreats a little more slowly. By late June seasonal ground frost melts to a depth of 30 cm—20 cm less than in the Betula papyrifera/Viburnum edule type. By August it is probably gone.

The flora found in stands of this community type are composed of 22–34 species. No taxa are unique to this type. American green alder flourishes; and Labrador-tea, twin-flower, and regeneration of black spruce may occur. On the other hand, this is the only type found on white spruce sites that lacks high bushcranberry and where prickly rose, though present, is not common. Table 5 lists the most important plant species found in this community type.

The mature stands are 50–130 years old and average about 600 trees/ha; less than 1 percent of these are white spruce. Regeneration is sparse (15 saplings/ha) and is mostly white spruce or black spruce, although some paper birch does occur. Beneath the trees, American green alder commonly forms a tall shrub layer 2–4 m in height averaging 4,000–5,000 stems/ha.

The forest floor is dominated by intermittent patches of low shrubs like mountain-cranberry and twin-flower; herbs like reedgrass; mosses like Hylocomium splendens, Polytrichum spp., and Dicranum spp.; and a continuous layer of litter. Small quantities of the following species also occur: fireweed, ground cedar, bunchberry, Pleurozium schreberi, and Cladonia spp.

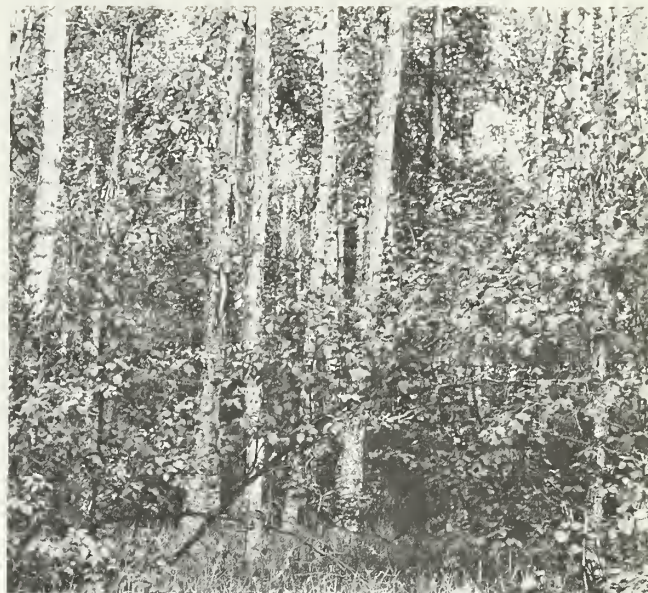


Figure 5.—A Betula papyrifera/Alnus crispa/Calamagrostis canadensis community. Paper birch in this stand (no. 172) are 140 years old.

In the absence of fire, stands of this type will succeed to open Picea glauca, P. mariana, or mixed P. glauca–P. mariana types.

The Betula papyrifera/Alnus crispa/Calamagrostis canadensis community type is synonymous with the closed deciduous type of the same name (Buckley and Libby 1957, Lutz 1956, Viereck 1975, and Viereck and Dyrness 1980). It is a component of the general birch type (Hutchison 1968, Neiland and Viereck 1979, and Viereck and Little 1972). On vegetation maps with scales of 1:2,500,000 and 1:7,500,000 it is one component of the even more generalized types: upland spruce–hardwood forest (Joint Federal–State Land Use Planning Commission for Alaska 1973), spruce–birch forest (Küchler 1966), and the moderately high, mixed evergreen and deciduous forest type (Spetzman 1963).

Table 5—Important plant species and litter components of the *Betula papyrifera*/*Alnus crispa*/*Calamagrostis canadensis* community type (Type 3) of interior Alaska

Species and litter component	Mature stands <u>1/</u>			
	Cover <u>2/</u>	Density <u>3/</u>	D.b.h. <u>4/</u>	Frequency <u>5/</u>
	<u>Percent</u>	<u>Stems/ha</u>	<u>Cm</u>	<u>Percent</u>
Tree layer:				
<i>Betula papyrifera</i> — Mature trees	—	600	16.2–21.0	100
<i>Picea glauca</i> — Seedlings	—	1,000	5.9–16.6	5
<i>Picea mariana</i> — Saplings	—	15	—	40
Tall shrub layer:				
<i>Alnus crispa</i>	—	4,800	—	40
Herb layer:				
<i>Calamagrostis</i> spp.	3	—	—	55
Mosses:				
<i>Hylocomium splendens</i>	3	—	—	50
<i>Polytrichum</i> spp.	2	—	—	42
Litter component:				
Leaves and twigs	92	—	—	100
Dead wood and fallen logs	7	—	—	100

1/ Number of stands sampled: 2; age: 50–130 years; number of species found: 22–34; depth of organic layer: 12–13 cm.

2/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. The values given are rounded to the nearest whole number.

3/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) \div total number of stands sampled. The values given above 200 are rounded to the nearest 100; the values below 100 are rounded to the nearest whole number.

4/ D.b.h. is the diameter of a tree at breast height. The mean stand d.b.h. value for a species is given; when more than 1 stand was sampled, the range of mean values is given.

5/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. The values given are rounded to the nearest whole number.

4. Picea glauca/Viburnum edule/Equisetum arvense/Hylocomium splendens community type

Mature stands of this type are characterized by a closed canopy of white spruce (Picea glauca) trees, an extensive tall shrub layer of prickly rose and high bushcranberry (Viburnum edule), and an extensive cover of field horsetail (Equisetum arvense) and the feathermoss Hylocomium splendens (fig. 6).

Stands typifying this community type occur on many south-facing slopes that vary in grade between 7 and 40 percent. They are most common at lower elevations, those below 610 m and on south-facing slopes associated with the larger river systems. The soil on these slopes consists of an 8- to 15-cm surface horizon of organic material over a deeper mantle of loess. The soil is not much different from that found on sites where quaking aspen and paper birch occur. Soil on these sites, however, is a little cooler than in most hardwood stands because the presence of a 10- to 15-cm thick moss layer insulates the ground from incoming solar radiation. Frost leaves the ground more slowly but is gone by August. By late June the soil has thawed to a minimum depth of 40 cm.

The flora in stands of this community type is composed of about 32 species. All species occurring in hardwood stands also occur in stands of this type but in different quantities. Table 6 lists the more important plant species found in this community type.

When the trees are 100-200 years old, the community is somewhat open and dominated by large white spruce trees. Data from this study show that tree densities average 500 stems/ha, diameters are 12- to 35-cm d.b.h., and heights are 20-30 m. Farr (1967) found the same characteristics for 150-year-old white spruce. Both white spruce and paper

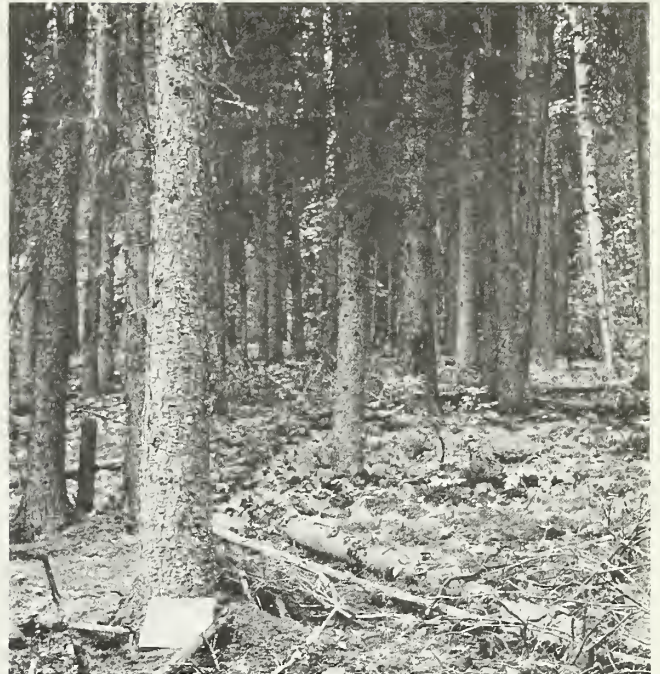


Figure 6.—A Picea glauca/Viburnum edule/Equisetum arvense/Hylocomium splendens community. White spruce trees in this stand (no. 312) are 120 years old.

birch occur in the understory. Hardwood snags and decaying logs occur on the forest floor. Prickly rose and high bushcranberry, both 1-1.5 m tall, form a well-developed tall shrub layer above which occasional clumps of American green alder extend 3-4 m tall. The forest floor is carpeted with an almost continuous layer of Hylocomium splendens 20-25 cm deep, occasional patches of twin-flower and Geocaulon lividum, and a scattering of field horsetail. Leaf litter occurs but is rapidly incorporated into the moss layer.

Table 6—Important plant species and litter components of the Picea glauca/Viburnum edule/Equisetum arvense/Hylocomium splendens community type (Type 4) of interior Alaska

Species and litter component	Mature stands 1/			
	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/
	Percent	Stems/ha	Cm	Percent
Tree layer:				
<u>Betula papyrifera</u> —				
Mature trees	—	40	21.0–24.0	25
Saplings	—	6	—	30
Seedlings	—	700	—	10
<u>Picea glauca</u> —				
Mature trees	—	500	27.3–30.6	100
Saplings	—	20	—	100
Seedlings	—	1,600	—	25
Fall shrub layer:				
<u>Rosa acicularis</u>	—	12,300	—	70
<u>Viburnum edule</u>	—	7,600	—	40
Herb layer:				
<u>Equisetum arvense</u>	4	—	—	80
<u>Geocaulon lividum</u>	4	—	—	55
Mosses:				
<u>Hylocomium splendens</u>	60	—	—	90
<u>Pleurozium schreberi</u>	5	—	—	25
Litter component:				
Leaves and twigs	25	—	—	95
Dead wood and fallen logs	15	—	—	60

1/ Number of stands sampled: 2; age: 150–200 years; number of species found: 31–33; depth of organic layer: 12 cm.

2/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) ÷ total number of stands sampled. The values given are rounded to the nearest whole number.

3/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) ÷ total number of stands sampled. The values given above 200 are rounded to the nearest 100; the values below 100 are rounded to the nearest whole number.

4/ D.b.h. is the diameter of a tree at breast height. The mean stand d.b.h. value for a species is given; when more than 1 stand was sampled, the range of mean values is given.

5/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) ÷ total number of stands sampled. The values given are rounded to the nearest whole number.

Many of these white spruce stands appear to have developed from the Populus tremuloides and Betula papyrifera community types already discussed. Some pure white spruce stands establish themselves immediately after fire, but this is not common. The establishment of white spruce depends on the presence of exposed mineral soil, viable seed, and adequate shade for young seedlings. None of these requirements are assured when white spruce stands are burned or otherwise disturbed (Zasada 1972). Stands of this type may slowly replace themselves or become open mixed white spruce-paper birch stands since both species occur in the understory. The existing trees are all younger than 300 years in age, however, and most show no sign of internal rotting so we do not know what happens in the next generation of communities of this type.

The Picea glauca/Viburnum edule/Equisetum arvense/Hylocomium splendens community type is synonymous with the closed Picea glauca/Viburnum edule/Equisetum arvense type (Viereck and Dyrness 1980; also see footnote 4). It is a major component of the more general white spruce or white spruce/feathermoss types (Buckley and Libby 1957, Hutchison 1968, Lutz 1956, Neiland and Viereck 1977; Viereck 1970, 1975; and Viereck and Little 1972). On vegetation maps with scales of 1:2,500,000 and 1:7,500,000, it is an important component of the following types: upland spruce-hardwood forest (Joint Federal-State Land Use Planning Commission for Alaska 1973), spruce-birch forest (Küchler 1966), and the high, evergreen spruce forest (Spetzman 1963).



Figure 7.—A Picea glauca/Rosa acicularis/Equisetum sylvaticum/Hylocomium splendens community. White spruce trees in this stand (no. 134) are 110 years old.

5. Picea glauca/Rosa acicularis/Equisetum sylvaticum/Hylocomium splendens community type

Mature stands of this type are characterized by a closed canopy of white spruce (Picea glauca) trees, an extensive tall shrub layer of prickly rose (Rosa acicularis), an almost continuous mat of feathermoss (primarily Hylocomium splendens), and extensive areas of woodland horsetail (Equisetum sylvaticum) on the forest floor (fig. 7).

Stands typifying this community type occur on flood plain islands or within one-half mile of active river channels. Periodic flooding of these sites causes the soil profiles to be stratified; layers of organic matter alternate with layers of silt, both overlying alluvial sand and gravel (Zasada 1972). In spring, soils thaw more slowly than on their upland counterparts. By late June the minimum depth of thaw is 30 cm—10 cm shallower than the depth of thaw on upland sites. By mid-July the soil on both upland and flood plain sites is completely free of seasonal frost (Viereck 1970). Flood plain sites are created, maintained, and destroyed by the deposition and erosion activities of meandering river channels. Water channels also help protect these areas from wildfire.

The flora in communities of this type is composed of about 30 species. No taxa are unique to these sites; however, the following reach their best development on these sites: white spruce, balsam poplar, prickly rose, thinleaf alder, twin-flower, and the feathermoss Rhytidiadelphus triquetrus. Data on the more important species are given in table 7. Stands of this community type are the most productive in interior Alaska; they contain up to 60 m³/ha of wood (Hutchison 1968, Viereck and Little 1972).

In mature stands 120–200 years old, the tree canopy is composed of mostly white spruce; however, balsam poplar and paper birch occur occasionally. Quaking aspen trees rarely grow on the flood plain. In these stands, tree densities average 500 stems/ha and diameters average 26.1–33.5-cm d.b.h. with the larger trees occurring in the older stands.

Beneath the trees, tall shrubs, low shrubs, herbs, and mosses are common. Prickly rose 2–3 m tall is everywhere and probably a good indicator of the productiveness of the sites.^{7/} High bushcranberry occurs but is less abundant than on upland sites; it appears to decrease as stand age increases. Hylocomium splendens blankets the forest floor, although other feathermosses, Pleurozium schreberi and Rhytidiadelphus triquetrus, are intermixed, as are patches of twin-flower, woodland horsetail, Geocaulon lividum, one-sided wintergreen, and liverleaf wintergreen.

If these sites are left undisturbed—not burned or undercut by the stream—and remain close to the active river channel, they will probably maintain themselves. If the active river channel moves away from the area, however, periodic flooding will become less frequent, allowing the moss layer to accumulate and thicken. When this happens, these permafrost-free areas will stagnate; they will slowly be invaded by black spruce, bog, and permafrost (Viereck 1970).

The Picea glauca/Rosa acicularis/Equisetum sylvaticum/Hylocomium splendens community type has been variously named: Picea glauca/Linnaea borealis/Equisetum sylvaticum (Viereck and Dyrness 1980; also see footnote 4), white spruce/rose/feathermoss (Neiland and Viereck 1977), and Picea glauca/feathermoss (Buckley and Libby 1957; Viereck 1970, 1975; Viereck and Dyrness 1980). On vegetation maps with scales of 1:2,500,000 and 1:7,500,000, it is called bottomland spruce–poplar forest type (Joint Federal–State Land Use Planning Commission for Alaska 1973), upland black spruce–white spruce forest type (Küchler 1966), and high, evergreen spruce forest type (Spetzman 1963).

^{7/}Personal communication with Francis Herman, Institute of Northern Forestry, Fairbanks, Alaska.

Table 7—Important plant species and litter components of the Picea glauca/Rosa acicularis/Equisetum sylvaticum/Hylocomium splendens community type (Type 5) of interior Alaska

Species and litter component	Mature stands 1/			
	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/
	Percent	Stems/ha	Cm	Percent
Tree layer:				
<u>Picea glauca</u> —				
Mature trees	—	500	26.1–33.5	100
Seedlings	—	1,800	—	30
Tall shrub layer:				
<u>Rosa acicularis</u>	—	16,000	—	82
<u>Viburnum edule</u>	—	2,600	—	40
Low shrub layer:				
<u>Linnaea borealis</u>	11	—	—	90
Herb layer:				
<u>Equisetum sylvaticum</u>	3	—	—	85
<u>Geocaulon lividum</u>	2	—	—	65
Mosses:				
<u>Hylocomium splendens</u>	60	—	—	95
<u>Pleurozium schreberi</u>	5	—	—	30
Litter component:				
Leaves and twigs	25	—	—	98
Dead wood and fallen logs	19	—	—	100

1/ Number of stands sampled: 2; age: 120–200 years; number of species found: 30; depth of organic layer: 5 cm.

2/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: $\text{Cover} = \Sigma (\text{mean stand cover value for a species}) \div \text{total number of stands sampled}$. The values given are rounded to the nearest whole number.

3/ The computed or counted number of stems occurring in a given area. It is based on the equation: $\text{Density} = \Sigma (\text{mean stand density value for a species}) \div \text{total number of stands sampled}$. The values given above 200 are rounded to the nearest 100; the values below 100 are rounded to the nearest whole number.

4/ D.b.h. is the diameter of a tree at breast height. The mean stand d.b.h. value for a species is given; when more than 1 stand was sampled, the range of mean values is given.

5/ The percent of plots in which a given species occurs. It is based on the equation: $\text{Frequency} = \Sigma (\text{mean stand frequency value for a species}) \div \text{total number of stands sampled}$. The values given are rounded to the nearest whole number.



Figure 8.—A Populus balsamifera/Oplopanax horridus community. Balsam poplar trees in this stand (no. 202) are 200 years old.

6. Populus balsamifera/Oplopanax horridus community type

Mature stands of this type are characterized by a closed canopy of mostly balsam poplar (Populus balsamifera) trees, extensive patches of devilsclub (Oplopanax horridus), and a scattering of shade tolerant herbs and ferns (fig. 8). Stands typifying this community type are restricted to flood plains on the south side of the Alaska Range. They are especially well developed near Talkeetna in the Susitna and Chulitna River valleys.

Soils on these sites are moist silt loams. Flooding is periodic, at least on the lower terraces. An organic layer 9–10 cm thick is striated with silt layers and overlies coarse sands and gravels of river origin. Snow usually remains on the ground until late May; consequently, soil temperatures are slow to warm and the seasonal soil frost is slow to melt.

The flora found in stands of this community type consists of about 24 species. No taxa are unique to these sites; however, species such as balsam poplar, devilsclub, clasping twisted-stalk, and spinulose shield-fern thrive. Table 8 lists the more important species of this community type.

Data from this study for stands 200 years old show an average of 140 trees/ha, a density low for hardwood types. These trees are large, however; balsam poplar average 35 m in height and 65.6-cm d.b.h., but trees up to 87-cm d.b.h. were measured. White spruce, the same age are smaller, only 32-cm d.b.h. and account for one-third of the tree density. Understory tree regeneration is lacking.

Table 8—Important plant species and litter components of the Populus balsamifera/Oplopanax horridus community type (Type 6) of interior Alaska

Species and litter component	Mature stands <u>1/</u>			
	Cover <u>2/</u>	Density <u>3/</u>	D.b.h. <u>4/</u>	Frequency <u>5/</u>
	<u>Percent</u>	<u>Stems/ha</u>	<u>Cm</u>	<u>Percent</u>
Tree layer:				
<u>Picea glauca</u> — Mature trees	—	40	32.0	60
<u>Populus balsamifera</u> — Mature trees	—	100	65.6	95
Tall shrub layer:				
<u>Oplopanax horridus</u>	—	24,100	—	100
Herb layer:				
<u>Dryopteris dilatata</u>	10	—	—	35
<u>Equisetum arvense</u>	5	—	—	95
<u>Galium triflorum</u>	1	—	—	70
<u>Pyrola asarifolia</u>	5	—	—	30
<u>Streptopus amplexifolius</u>	7	—	—	85
Litter component:				
Leaves and twigs	94	—	—	100
Dead wood and fallen logs	3	—	—	70

1/ Number of stands sampled: 1; age: 200 years; number of species found: 24; depth of organic layer: 9 cm.

2/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. The values given are rounded to the nearest whole number.

3/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) \div total number of stands sampled. The values given above 200 are rounded to the nearest 100; the values below 100 are rounded to the nearest whole number.

4/ D.b.h. is the diameter of a tree at breast height. The mean stand d.b.h. value for a species is given; when more than 1 stand was sampled, the range of mean values is given.

5/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. The values given are rounded to the nearest whole number.

Other vegetation occurs beneath the trees. Devilclub grows 1-2 m in height and dominates the tall shrub layer, but patches of thinleaf alder may extend even higher, and high bushcranberry and prickly rose occur in openings. The low shrub and herb layers are discontinuous. Currants (Ribes spp.), which sometime grow at the base of trees, are the only low shrub species found; spinulose shield-fern and clasping twisted-stalk are the most extensive of the herb species.

Regeneration of this community type is little understood. The balsam poplar will probably die first. Many already have rotten centers (Zasada and others 1981). Open white spruce stands will remain for awhile; however, the lack of understory regeneration of any tree species in today's stands does not aid in speculations for the future. North of the Alaska Range, white spruce almost always succeeds balsam poplar on flood plains.

The Populus balsamifera/Oplopanax horridus community type is probably a south-central Alaska version of the more general Populus balsamifera/Alnus tenuifolia/Calamagrostis canadensis type mentioned or discussed by Buckley and Libby (1957), Hettinger and Janz (1974), Lutz (1956), Neiland and Viereck (1977), Viereck (1970, 1975), and Viereck and Dyrness (1980). On vegetation maps with scales of 1:2,500,000 and 1:7,500,000, this community type is included in the following types: bottomland spruce-poplar forest (Joint Federal-State Land Use Planning Commission for Alaska 1973), spruce-birch forest (Küchler 1966), and high evergreen spruce forest (Spetzman 1963).

Black Spruce Sites

Black spruce sites occur in areas of poor drainage, on north-facing slopes within 8 km of major rivers, or on upland slopes of all exposures more distant from rivers where white spruce is absent. These sites are usually cool, and permafrost is common. Soils tend to be wet Inceptisols. The soil thaws to a depth of 20-90 cm every summer and, in general, the thicker the moss layer, the more shallow the permafrost layer.

The vegetation is dominated by trees, but low shrubs, mosses, and sometimes lichens are also prominent. Black spruce, quaking aspen, paper birch, Alaska larch, mountain-cranberry, bog blueberry, the mosses Pleurozium schreberi and Sphagnum spp., and lichens Cladonia spp. and Cladonia spp. grow prominently on black spruce sites. Occasionally white spruce is also found. Together they produce the numerous forest types that occur on black spruce sites.

Six of these forest types will be described (table 2, types 7-12). Of the six, four (types 7-10) tend to occur on mesic upland slopes, one (type 11) occurs on cool, mesic to moist timberline sites, and one (type 12) occurs on cool, moist valley bottoms and north-facing sites. The types can intermix to a degree, except for quaking aspen, which is limited to warm, well-drained sites. These six mature community types occur extensively throughout the Alaska taiga but do not preclude the existence of other community types; for example, the black spruce-American larch community type which is not discussed in this paper.

7. Populus tremuloides-Picea mariana/Cornus canadensis community type

Mature stands of this type are characterized by a closed canopy dominated by quaking aspen (Populus tremuloides); black spruce (Picea mariana) grows in the understory. Low shrubs, especially mountain-cranberry and bunchberry (Cornus canadensis), dominate on the forest floor (fig. 9).

Stands typifying this community type occur on warm, well-drained black spruce sites; i.e., on slopes with southerly exposures or on slightly raised, better drained areas on upland valley floors. The organic layer is shallow, about 12 cm, and overlies loess, bedrock, or river alluvium. By late June the seasonal soil frost melts to a depth of 50–60 cm, and by August, when the seasonal frost is gone, pockets of permafrost may occur 65 cm or more below the surface.

The flora found in communities of this type is moderately rich; 31–36 species were present in each of the stands studied. No taxa are unique to this community type. Species such as quaking aspen, high bushcranberry, twin-flower, bearberry, and fireweed occur more abundantly in communities of this type than in communities of Picea mariana types. The flora in communities of this type does even better in quaking aspen communities growing on white spruce sites. Table 9 gives information about the species that occur most frequently.

The quaking aspen and black spruce trees in this community type reach maturity when they are 60–70 years old. Data from the study show that tree densities average 1,500 stems/ha for quaking aspen and 400 stems/ha for black spruce. Diameters average 12.9- to 13.9-cm d.b.h. for quaking aspen and 6.1- to 6.6-cm d.b.h. for black spruce. Heights average 10–15 m for quaking aspen and 4–12 m for black spruce.



Figure 9.—A Populus tremuloides-Picea mariana/Cornus canadensis community. Quaking aspen trees in this stand (no. 176) are 50 years old.

Beneath the trees an intermittent tall shrub layer is dominated by prickly rose 0.5–1 m tall; however, clumps of American green alder or Bebb willow 2–4 m tall occur occasionally. Low shrubs of mountain-cranberry, bog blueberry, and Labrador-tea along with feather-mosses Hylocomium splendens and Pleurozium schreberi, and the herbs bunchberry, reed-grass, and tall bluebell cover the forest floor. Except in the clumps of moss, the extensive litter layer and rotting quaking aspen logs are visible on the forest floor.

Table 9—Important plant species and litter components of the Populus tremuloides-Picea mariana/Cornus canadensis community type (Type 7) of interior Alaska

Species and litter component	Mature stands 1/				Overmature stands 6/			
	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/
	Percent	Stems/ha	Cm	Percent	Percent	Stems/ha	Cm	Percent
Tree layer:								
<u>Picea mariana</u> —								
Mature trees	—	400	6.1-6.6	55	—	2,000	6.1-7.2	100
Saplings	—	40	—	90	—	60	—	95
Seedlings	—	9,400	—	60	—	14,300	—	75
<u>Populus tremuloides</u> —								
Mature trees	—	1,500	12.9-13.9	95	—	25	23.9	10
Seedlings	—	2,000	—	30	—	—	—	—
Tall shrub layer:								
<u>Rosa acicularis</u>	—	3,600	—	45	—	4,400	—	90
Low shrub layer:								
<u>Vaccinium uliginosum</u>	3	—	—	55	12	—	—	85
<u>Vaccinium vitis-idaea</u>	15	—	—	80	5	—	—	95
Herb layer:								
<u>Calamagrostis</u> spp.	1	—	—	60	1	—	—	70
<u>Cornus canadensis</u>	6	—	—	95	1	—	—	38
Mosses:								
<u>Hylocomium splendens</u>	7	—	—	45	54	—	—	85
<u>Pleurozium schreberi</u>	3	—	—	30	16	—	—	40
Lichen:								
<u>Peltigera canina</u>	7/	—	—	5	4	—	—	60
Litter component:								
Leaves and twigs	85	—	—	100	28	—	—	100
Dead wood and fallen logs	6	—	—	85	4	—	—	65

- 1/ Number of mature stands sampled: 2; age: 65-70 years; number of species found: 31-36; depth of organic layer: 10-15 cm; depth of active thaw layer: 60 cm and over.
- 2/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: $\text{Cover} = \frac{\Sigma (\text{mean stand cover value for a species})}{\text{total number of stands sampled}}$. The values given are rounded to the nearest whole number.
- 3/ The computed or counted number of stems occurring in a given area. It is based on the equation: $\text{Density} = \frac{\Sigma (\text{mean stand density value for a species})}{\text{total number of stands sampled}}$. The values given above 200 are rounded to the nearest 100; the values below 100 are rounded to the nearest whole number.
- 4/ D.b.h. is the diameter of a tree at breast height. The mean stand d.b.h. value for a species is given; when more than 1 stand was sampled, the range of mean values is given.
- 5/ The percent of plots in which a given species occurs. It is based on the equation: $\text{Frequency} = \frac{\Sigma (\text{mean stand frequency value for a species})}{\text{total number of stands sampled}}$. The values given are rounded to the nearest whole number.
- 6/ Number of overmature stands sampled: 2; age: 65-120 years; number of species found: 33; depth of organic layer: 13-17 cm; depth of active thaw layer: 45-90 cm and over.
- 7/ Less than 0.5 percent.

As stands in this community type age, the quaking aspen trees die, fall, and decay, whereas the amount of feathermoss increases (see table 9). Soon little evidence is left of the quaking aspen, and the community evolves into one in the Picea mariana/feathermoss community type. If a fire burns a stand in the Populus tremuloides-Picea mariana/Cornus canadensis community type, the stand becomes self-perpetuating. Quaking aspen and low shrubs develop from root suckers and black spruce from seeds, but the faster growing quaking aspen soon dominate again.

The Populus tremuloides-Picea mariana/Cornus canadensis community types have been variously named. This name was first used by Foote (see footnote 4) and later by Viereck and Dyrness (1980). Neiland and Viereck (1977) mention it as part of the aspen type. Most authors consider it part of the more general closed spruce-hardwood forest type (Neiland and Viereck 1977, Viereck and Dyrness 1980, Viereck and Little 1972). On vegetation maps with scales of 1:2,500,000 and 1:7,500,000, it is a component of the following types: upland spruce-hardwood (Joint Federal-State Land Use Planning Commission for Alaska 1973), spruce-birch (Küchler 1966), and moderately high, mixed evergreen and deciduous forest (Spetzman 1963).



Figure 10.—A Picea mariana-Betula papyrifera/Vaccinium uliginosum-Ledum groenlandicum community. Black spruce and paper birch trees in this stand (no. 179) are 80–100 years old.

8. Picea mariana-Betula papyrifera/Vaccinium uliginosum-Ledum groenlandicum community type

Mature stands of this type are characterized by a closed canopy of black spruce (Picea mariana) and paper birch (Betula papyrifera); a discontinuous understory of low shrubs, mostly mountain-cranberry, Labrador-tea (Ledum groenlandicum), and bog blueberry (Vaccinium uliginosum); and a developing cover of feather-mosses, mostly Pleurozium schreberi, on the forest floor (fig. 10).

Stands typifying this community type can be found wherever mesic black spruce sites occur; i.e., on slopes of all aspects or on valley bottoms where a modest amount of drainage occurs. Permafrost may or may not be present. By July the ground thaws to a maximum depth of 50 cm. These sites, therefore, may have slightly cooler soil temperatures than sites where the Populus tremuloides-Picea mariana/Cornus canadensis community type occurs.

The flora found in communities of this type is fairly diverse; it contains 32-34 species. There are no species unique to the community type. Instead, the flora is a mixture of taxa; some represent species that do very well on warm, well-drained sites and others do very well on cooler, moderately drained sites. As the community reaches overmaturity, the number of species drops to 23-25 per stand. Table 10 gives information on the species occurring most frequently.

When trees in stands of this community type are 40-70 years old, black spruce average 900 trees/ha, 6.9-8.7-cm d.b.h. and 2-17 m in height. Saplings, and especially seedlings, are numerous. Paper birch, on the other hand, are larger (up to 18.3-cm d.b.h.), fewer in number (only 300 trees/ha), about the same height, but with little reproduction. By the time these stands are 120 years old, they are overmature. Most of the paper birch die, leaving behind black spruce trees 11.4- to 14.8-cm d.b.h.

Beneath these trees, there may or may not be a tall shrub layer but a low shrub layer is always there. When present, the tall shrub layer consists of prickly rose and American green alder. Both these species continue to do well in overmature stands. The low shrub layer is always represented by mountain-cranberry, bog blueberry, and Labrador-tea, and in some stands also by crowberry.

The forest floor is mainly covered by a developing blanket of feathermoss in which patches of herbs and lichens may occur. The feathermoss Pleurozium schreberi dominates in 70-year-old stands, where it covers 35 percent of the area, whereas Pleurozium schreberi and Hylocomium splendens share dominance in 120-year-old stands, where they cover 54 and 20 percent of the forest floor. Herbs may or may not be present; however, reedgrass occurs in most stands. Soil lichens (Cladonia spp.) occur but are not abundant. Fallen logs, mostly of paper birch, decay rapidly leaving hollow bark cylinders to be overgrown by feathermoss.

In the absence of fire, communities of this type slowly lose their paper birch element; their black spruce component then becomes pure and the community type changes to one of the Picea mariana types. With the help of fire, stands in this community type maintain themselves. Since fires reburn most areas on a cycle of less than 100 years, stands of this community type are both common and extensive.

The Picea mariana-Betula papyrifera/Vaccinium uliginosum-Ledum groenlandicum community type is one of the closed spruce-birch types (Viereck and Dyrness 1980) and is probably synonymous with their Picea mariana-Betula papyrifera/Ledum type. On vegetation maps with scales of 1:2,500,000 and 1:7,500,000, it is a component of the following types: upland spruce-hardwood forest, and lowland spruce-hardwood forest (Joint Federal-State Land Use Planning Commission for Alaska 1973); spruce-birch forest, and black spruce forest (Küchler 1966); and moderately high, mixed evergreen and deciduous forest, and low, mixed evergreen and deciduous forest (Spetzman 1963).

Table 10—Important plant species and litter components of the Picea mariana-Betula papyrifera/Vaccinium uliginosum-Ledum groenlandicum community type (Type 8) of interior Alaska

Species and litter component	Mature stands 1/				Overmature stands 6/			
	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/
	Percent	Stems/ha	Cm	Percent	Percent	Stems/ha	Cm	Percent
Tree layer:								
<u>Betula papyrifera</u> —								
Mature trees	—	300	5.8–18.3	45	—	70	16.0–25.2	10
<u>Picea mariana</u> —								
Mature trees	—	900	6.9–8.7	85	—	1,700	11.4–14.8	100
Saplings	—	200	—	90	—	900	—	100
Seedlings	—	7,000	—	65	—	1,600	—	70
Tall shrub layer:								
<u>Alnus crispa</u>	—	800	—	10	—	2,800	—	40
<u>Rosa acicularis</u>	—	900	—	30	—	4,000	—	35
Low shrub layer:								
<u>Ledum groenlandicum</u>	5	—	—	55	1	—	—	8
<u>Vaccinium uliginosum</u>	3	—	—	55	3	—	—	50
<u>Vaccinium vitis-idaea</u>	5	—	—	80	11	—	—	100
Herb layer:								
<u>Calamagrostis</u> spp.	1	—	—	20	6	—	—	9
Mosses:								
<u>Hylocomium splendens</u>	2	—	—	35	20	—	—	75
<u>Pleurozium schreberi</u>	35	—	—	85	54	—	—	100
<u>Polytrichum</u> spp.	2	—	—	50	1	—	—	25
Litter component:								
Leaves and twigs	60	—	—	100	16	—	—	100
Dead wood and fallen logs	5	—	—	75	9	—	—	100

- 1/ Number of mature stands sampled: 3; age: 40-70 years; number of species found: 32-34; depth of organic layer: 16-18 cm; depth of active thaw layer: 45 cm, July.
- 2/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: $\text{Cover} = \frac{\Sigma (\text{mean stand cover value for a species})}{\text{total number of stands sampled}}$. The values given are rounded to the nearest whole number.
- 3/ The computed or counted number of stems occurring in a given area. It is based on the equation: $\text{Density} = \frac{\Sigma (\text{mean stand density value for a species})}{\text{total number of stands sampled}}$. The values given above 200 are rounded to the nearest 100; the values below 100 are rounded to the nearest whole number.
- 4/ D.b.h. is the diameter of a tree at breast height. The mean stand d.b.h. value for a species is given; when more than 1 stand was sampled, the range of mean values is given.
- 5/ The percent of plots in which a given species occurs. It is based on the equation: $\text{Frequency} = \frac{\Sigma (\text{mean stand frequency value for a species})}{\text{total number of stands sampled}}$. The values given are rounded to the nearest whole number.
- 6/ Number of overmature stands sampled: 2; age: 100-120 years; number of species found: 23-25; depth of organic layer: 13-14 cm; depth of active thaw layer: 50 cm, July.



Figure 11.—A Picea mariana/Vaccinium uliginosum-Ledum groenlandicum/Pleurozium schreberi community. Black spruce trees in this stand (no. 175) are 50 years old.

9. Picea mariana/Vaccinium uliginosum-Ledum groenlandicum/Pleurozium schreberi community type

Mature stands of this type are characterized by dense black spruce (Picea mariana) with an understory of low shrubs and moss. Labrador-tea (Ledum groenlandicum), mountain-cranberry, and bog blueberry (Vaccinium uliginosum) dominate the low shrub layer; the feathermosses Pleurozium schreberi and Hylocomium splendens dominate the moss layer (fig. 11).

Stands typifying this community type may be found on all mesic black spruce sites; i.e., on both slopes and valley bottoms whenever the soil is not too wet. Usually a 5- to 25-cm-thick surface horizon of organic material overlies a layer of loess, stony residual soil, or valley alluvium. Ice-rich permafrost is generally present. The surface soil is kept cool and moist by the permafrost below and the moss insulation above. Surface soil temperatures increase throughout the summer; the soil thaws to a depth of 30 cm by late June and to 50 cm by August.

The flora found in communities of this type is composed of 28-35 species. No taxa are unique to the community type, and some species are absent. Hardwoods and lichens, distinctive of other Picea mariana types, are essentially under-represented in this community type. Table II gives information on the species occurring most frequently.

When the trees are 40–60 years old, the vegetation in communities of this type is established. Data from this study show that trees—mostly black spruce—average 1,200 to 3,700 stems/ha, 4.3– to 5.6–cm d.b.h., and 3–9 m tall. Older black spruce trees occur alone or in stringers. Some have fire scars showing they date to a preburn era. Smaller saplings, seedlings, and layerings are also numerous.

Beneath the trees, shrubs—mainly Labrador-tea, bog blueberry, mountain-cranberry, and prickly rose—form a discontinuous layer that grows to 1 m in height. Mosses cover the ground to a depth of 20 cm in most areas but up to 100 cm where mounds of *Sphagnum* spp. occur. American green alder and resin birch (*Betula glandulosa*) are sometimes common. *Pleurozium schreberi* covers about one-half of the forest floor, but other mosses—*Hylocomium splendens*, *Polytrichum* spp., and *Sphagnum* spp.—are important. Lichens, primarily *Cladonia rangiferina*, and herbs—mostly reedgrass, cloudberry, and woodland horsetail—are lightly scattered throughout the moss layer.

Stands dominated by trees older than 100 years in age occur, but usually as stringers or islands within younger stands. Most of these areas also have a second age class of trees that is younger than 100 years suggesting that they have been lightly disturbed or otherwise influenced by the disturbances occurring around them. In any event, these older stands are similar to the younger stands but show the influence of time; the trees are larger in diameter (17–cm d.b.h.), less dense (averaging 2,000 stems/ha), and slightly taller (11 m). Low

shrubs and *Sphagnum* spp. moss cover more area, whereas tall shrubs cover less area. In addition, the feathermoss layer, which is continuous in both young and old stands, is thicker. Black spruce seedlings occur, but reproduction is primarily by layering. It appears that in the absence of fire, stands of this community type will maintain themselves; however, most stands burn before they are 100 years old. When fire occurs, root systems and seeds in cones are generally not consumed by fire, so stands are quick to recover.

The *Picea mariana*/*Vaccinium uliginosum*–*Ledum groenlandicum*/*Pleurozium schreberi* community type has been variously named: *Picea mariana*/*Vaccinium*/feathermoss (Lutz 1956; Viereck 1975, 1979; Viereck and Dyrness 1980); *Picea mariana*/*Ledum groenlandicum*/*Equisetum sylvaticum* (see footnote 4); and open, low-growing spruce (Viereck and Little 1972). On vegetation maps with scales of 1:2,500,000 and 1:7,500,000, it is a component of the following types: upland and lowland spruce–hardwood forest (Joint Federal–State Land Use Planning Commission for Alaska 1973), black spruce forest (Küchler 1966), and both the moderately high and the low, mixed evergreen and deciduous forests (Spetzman 1963).

Table 11—Important plant species and litter components of the Picea mariana/Vaccinium uliginosum-Ledum groenlandicum/Pleurozium schreberi community type (Type 9) of interior Alaska

Species and litter component	Mature stands 1/				Overmature stands 6/			
	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/
	Percent	Stems/ha	Cm	Percent	Percent	Stems/ha	Cm	Percent
Tree layer:								
<u>Picea mariana</u> —								
Mature trees	—	2,700	4.3–5.6	100	—	2,000	17.0	100
Saplings	—	1,800	—	100	—	600	—	100
Seedlings	—	15,300	—	90	—	9,600	—	85
Low shrub layer:								
<u>Empetrum nigrum</u>	—	—	—	—	6	—	—	65
<u>Ledum groenlandicum</u>	8	—	—	80	17	—	—	95
<u>Vaccinium uliginosum</u>	11	—	—	90	7	—	—	95
<u>Vaccinium vitis-idaea</u>	15	—	—	100	20	—	—	100
Herb layer:								
<u>Calamagrostis</u> spp.	2	—	—	80	1	—	—	40
<u>Equisetum sylvaticum</u>	1	—	—	25	9	—	—	90
<u>Rubus chamaemorus</u>	2	—	—	35	7	—	—	90
Mosses:								
<u>Hylocomium splendens</u>	5	—	—	50	42	—	—	90
<u>Pleurozium schreberi</u>	47	—	—	95	24	—	—	85
<u>Polytrichum</u> spp.	15	—	—	60	6	—	—	75
<u>Sphagnum</u> spp.	12	—	—	31	21	—	—	75
Lichens:								
<u>Cladonia arbuscula</u>	1	—	—	10	2	—	—	60
<u>Cladonia rangiferina</u>	4	—	—	40	3	—	—	55
Litter component:								
Leaves and twigs	12	—	—	100	9	—	—	100
Dead wood and fallen logs	5	—	—	90	1	—	—	80

- 1/ Number of mature stands sampled: 5; age: 40–70 years; number of species found: 28–35; depth of organic layer: 18–21 cm; depth of active thaw layer: 35–50 cm.
- 2/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: $\text{Cover} = \frac{\Sigma (\text{mean stand cover value for a species})}{\text{total number of stands sampled}}$. The values given are rounded to the nearest whole number.
- 3/ The computed or counted number of stems occurring in a given area. It is based on the equation: $\text{Density} = \frac{\Sigma (\text{mean stand density value for a species})}{\text{total number of stands sampled}}$. The values given above 200 are rounded to the nearest 100; the values below 100 are rounded to the nearest whole number.
- 4/ D.b.h. is the diameter of a tree at breast height. The mean stand d.b.h. value for a species is given; when more than 1 stand was sampled, the range of mean values is given.
- 5/ The percent of plots in which a given species occurs. It is based on the equation: $\text{Frequency} = \frac{\Sigma (\text{mean stand frequency value for a species})}{\text{total number of stands sampled}}$. The values given are rounded to the nearest whole number.
- 6/ Number of overmature stands sampled: 1; age: 80–170 years; number of species found: 29; depth of organic layer: 18 cm; depth of active thaw layer: 50 cm.



Figure 12.—A *Picea mariana*/feathermoss-lichen community. This stand (no. 490) is 60 years old.

10. *Picea mariana*/feathermoss-lichen community type

In mature stands of this type, lichen-dominated openings separate the black spruce (*Picea mariana*) trees, which frequently occur in small, dense clumps. Low shrubs, mosses (primarily the feathermoss *Pleurozium schreberi*), and lichens grow beneath the trees and extend into the openings (fig. 12).

Stands typifying this community type occur wherever black spruce sites are found; i.e., on slopes of all aspects and gradients and on valley bottoms. A surface horizon of organic material overlies loess, weathered bedrock, or valley alluvium. The depth of the organic layer varies from 5 cm in the lichen-dominated openings to 20 cm in the moss and tree-dominated areas. Permafrost may or may not be present. Snow disappears from the tree bases and sunny openings first and is usually gone by late May. Soils continue to warm throughout the summer, and by August, seasonal soil frost is gone. During dry periods, the lichens become dessicated and brittle.

The flora of this community type include 29–38 species, making it moderately diverse to rich. No taxa is unique to this type, but it is the lichen element that makes this community type distinctive. Table 12 gives information about the species which occur most frequently.

When the black spruce trees are 40–70 years old, they average 2,900 stems/ha, 4.3– to 6.2-cm d.b.h., and 2–9 m tall. Black spruce saplings average 2,000 stems/ha and seedlings another 12,000 stems/ha. Despite these densities, which are many times those of the closed-canopied stands already discussed, stands in this community type have an intermittent overstory canopy. Clumping of trees within the stand and the narrow, triangular form of black spruce together create the open canopy.

Beneath the trees is the same vegetation as occurs in the Picea mariana/Vaccinium uliginosum-Ledum groenlandicum/Pleurozium schreberi type plus numerous lichens.

Nephroma arcticum forms extensive patches, especially in forest openings. Other lichens, primarily Cladonia rangiferina, C. arbuscula, Peltigera aphthosa, and Cetraria islandica, occur both in openings and beneath the trees. Together, the lichens cover 20 percent of the forest floor. Moss covers most of the forest floor; however, Sphagnum spp., if present, occur in very small patches.

Black spruce regeneration, both seedlings and layerings, occurs in sufficient quantities (12,000 stems/ha) to retain the forest canopy. The lichen patches show little evidence of being invaded by spruce. So in the absence of fire, stands of this community type will succeed themselves as long as the lichens survive.

It is uncertain how long that is. The oldest stand located was 70 years old. The lichens dry out almost as fast as the humidity of the air drops, making them highly flammable. Perhaps fire prevents stands of this community type from aging. Or perhaps the moss mat thickens as the stand ages, as it does in the Picea mariana/Vaccinium uliginosum-Ledum groenlandicum/Pleurozium schreberi community type, and the mosses simply overtop and kill the lichens. More study is needed.

The Picea mariana/feathermoss-lichen community type has been called Picea mariana/lichen (see footnote 4) and open Picea mariana/feathermoss-Cladonia (Viereck 1975, 1979; Viereck and Dyrness 1980). The woodland Picea mariana/Cladonia type (Viereck 1975, Viereck and Dyrness 1980) is closely related. It is certainly a component of the more general types: black spruce (Lutz 1956), muskeg (Buckley and Libby 1957), and open, low-growing spruce (Viereck and Little 1972). On vegetation maps with scales of 1:2,500,000 and 1:7,500,000, it is included in the following types: upland and lowland spruce-hardwood forest (Joint Federal-State Land Use Planning Commission for Alaska 1973), black spruce and spruce-birch forest (Küchler 1966), and both the moderately high and the low, mixed evergreen and deciduous forests (Spetzman 1963).

Table 12—Important plant species and litter components of the *Picea mariana*/feathermoss-lichen community type (Type 10) of interior Alaska

Species and litter component	Mature stands 1/			
	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/
	Percent	Stems/ha	Cm	Percent
Tree layer:				
<i>Picea mariana</i> —				
Mature trees	—	2,900	4.3–6.2	100
Saplings	—	2,000	—	100
Seedlings	—	12,000	—	90
Low shrub layer:				
<i>Ledum groenlandicum</i>	6	—	—	80
<i>Vaccinium uliginosum</i>	8	—	—	70
<i>Vaccinium vitis-idaea</i>	11	—	—	100
Herb layer:				
<i>Calamagrostis</i> spp.	1	—	—	40
<i>Geocaulon lividum</i>	1	—	—	45
Mosses:				
<i>Dicranum</i> spp.	3	—	—	60
<i>Hylocomium splendens</i>	11	—	—	50
<i>Pleurozium schreberi</i>	46	—	—	95
<i>Polytrichum</i> spp.	5	—	—	70
Lichens:				
<i>Cetraria islandica</i>	1	—	—	50
<i>Cladina arbuscula</i>	3	—	—	38
<i>Cladina rangiferina</i>	7	—	—	60
<i>Nephroma arcticum</i>	4	—	—	30
<i>Peltigera aphthosa</i>	3	—	—	60
Litter component:				
Leaves and twigs	13	—	—	95
Dead wood and fallen logs	8	—	—	85

1/ Number of stands sampled: 6; age: 40–70 years; number of species found: 29–38; depth of organic layer: 12–18 cm; depth of active thaw layer: 54–99 cm and over.

2/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. The values given are rounded to the nearest whole number.

3/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) \div total number of stands sampled. The values given above 200 are rounded to the nearest 100; the values below 100 are rounded to the nearest whole number.

4/ D.b.h. is the diameter of a tree at breast height. The mean stand d.b.h. value for a species is given; when more than 1 stand was sampled, the range of mean values is given.

5/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. The values given are rounded to the nearest whole number.

11. Picea mariana-Picea glauca/Betula glandulosa/lichen community type

Stands of this type are usually woodlands. Interspersed with the trees are numerous tall shrubs; low shrubs, mosses, and lichens cover the ground surface (fig. 13).

Stands typifying this community type occur on east- or west-facing slopes above 700 m or near timberline. These slopes are cool and dry to mesic. A thin surface layer of organic material 0-3 cm thick overlies stony soils and shallow bedrock.

The flora of these communities is a diverse mixture of taxa found on white spruce, black spruce, or alpine sites. No species are unique; however, resin birch (Betula glandulosa), the hybrid birch (Betula glandulosa X B. papyrifera), and lichens do particularly well. Table 13 gives information on the most common species found in this community type.

The timberline forest stands sampled were of mixed age. Trees 55 years old were mixed in approximately equal numbers with trees 110 and 195 years old. The canopy in this community is open, averaging 400 trees/ha, and composed of a mixture of white spruce (Picea glauca) and black spruce (Picea mariana). Sometimes there is more white than black spruce, at other times the reverse is true. Younger trees of both species exist, but they seem to be primarily black spruce. These stand 3-7 m tall and range from 7.6- to 10.9-cm d.b.h.; however, trees 32-cm d.b.h. are present occasionally.



Figure 13.—A Picea mariana-Picea glauca/Betula glandulosa/lichen community. Spruce trees in this stand (no. 244) are 130 years old.

Beneath the trees, resin birch, which grows to a height of 1.2 m, forms an almost continuous tall shrub layer. Clumps of hybrid birch and grayleaf willow occasionally stand above the resin birch with prickly rose sparsely scattered below.

Table 13—Important plant species and litter components of the Picea mariana-Picea glauca/Betula glandulosa/lichen community type (Type 11) of interior Alaska

Species and litter component	Mature stands 1/			
	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/
	Percent	Stems/ha	Cm	Percent
Tree layer:				
<u>Picea glauca</u> —				
Mature trees	—	140	8.5–10.9	60
Saplings	—	50	—	75
Seedlings	—	400	—	10
<u>Picea mariana</u> —				
Mature trees	—	260	7.6–9.5	90
Saplings	—	75	—	100
Seedlings	—	1,400	—	30
Tall shrub layer:				
<u>Betula glandulosa</u>	—	19,800	—	70
<u>Rosa acicularis</u>	—	1,500	—	30
Low shrub layer:				
<u>Empetrum nigrum</u>	4	—	—	40
<u>Ledum groenlandicum</u>	5	—	—	60
<u>Vaccinium uliginosum</u>	23	—	—	100
<u>Vaccinium vitis-idaea</u>	24	—	—	100
Herb layer:				
<u>Calamagrostis</u> spp.	2	—	—	60
Mosses:				
<u>Aulacomnium palustre</u>	3	—	—	40
<u>Dicranum</u> spp.	6	—	—	50
<u>Hylocomium splendens</u>	12	—	—	55
<u>Pleurozium schreberi</u>	23	—	—	70
<u>Polytrichum</u> spp.	5	—	—	90

See footnotes at end of table.

Table 13—Important plant species and litter components of the Picea mariana-Picea glauca/Betula glandulosa/lichen community type (Type 11) of interior Alaska (continued)

Species and litter component	Mature stands <u>1/</u>			
	Cover <u>2/</u>	Density <u>3/</u>	D.b.h. <u>4/</u>	Frequency <u>5/</u>
	<u>Percent</u>	<u>Stems/ha</u>	<u>Cm</u>	<u>Percent</u>
Lichens:				
<u>Cetraria cucullata</u>	4	—	—	85
<u>Cetraria islandica</u>	2	—	—	75
<u>Cetraria richardsonii</u>	2	—	—	40
<u>Cladina arbuscula</u>	8	—	—	80
<u>Cladina rangiferina</u>	4	—	—	85
<u>Cladonia gracilis</u>	1	—	—	40
<u>Peltigera aphthosa</u>	5	—	—	70
<u>Peltigera canina</u>	5	—	—	65
Litter component:				
Leaves and twigs	26	—	—	100
Dead wood and fallen logs	15	—	—	100

1/ Number of stands sampled: 2; age: 55–100; 195 years; number of species found: 38–53; depth of organic layer: 1–2 cm; depth of active thaw layer: no data; ground too rocky to probe.

2/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: $\text{Cover} = \Sigma (\text{mean stand cover value for a species}) \div \text{total number of stands sampled}$. The values given are rounded to the nearest whole number.

3/ The computed or counted number of stems occurring in a given area. It is based on the equation: $\text{Density} = \Sigma (\text{mean stand density value for a species}) \div \text{total number of stands sampled}$. The values given above 200 are rounded to the nearest 100; the values below 100 are rounded to the nearest whole number.

4/ D.b.h. is the diameter of a tree at breast height. The mean stand d.b.h. value for a species is given; when more than 1 stand was sampled, the range of mean values is given.

5/ The percent of plots in which a given species occurs. It is based on the equation: $\text{Frequency} = \Sigma (\text{mean stand frequency value for a species}) \div \text{total number of stands sampled}$. The values given are rounded to the nearest whole number.

Beneath the shrubs are a well-developed low shrub layer and an extensive lichen layer. Herbs and mosses occur but are scattered. Mountain-cranberry and bog blueberry, the two species found on all black spruce sites, continue to dominate the low shrubs although Labrador-tea, crowberry, and beauverd spirea occur. No single lichen species dominates; however the following lichens were present in all the stands studied: Cetraria cucullata, C. islandica, C. richardsonii, Cladina arbuscula, C. rangiferina, Cladonia gracilis, Peltigera aphthosa, and P. canina. The herb and moss species that commonly intermix with the more dominant vegetation on the forest floor include reedgrass, the feathermosses Pleurozium schreberi and Hylocomium splendens, Polypodium spp., Dicranum spp., and Aulacomnium palustre.

Stands of this community type appear able to maintain themselves. The 50- to 100-year break in tree age classes suggests that fires occur every 50-70 years. The presence of older trees and young white spruce suggests that the burns are not severe or that they leave numerous unburned islands in which the white spruce, mosses, and lichens survive.

The Picea mariana-Picea glauca/Betula glandulosa/lichen type is synonymous with the woodland Picea glauca-Picea mariana/lichen type (Vioreck and Dyrness 1980; also see footnote 4) and related to the open Picea mariana-Picea glauca/Betula glandulosa type (Vioreck 1979, Vioreck and Dyrness 1980). On vegetation maps with scales of 1:2,500,000 and 1:7,500,000, it is a component of the following types: upland spruce-hardwood forest (Joint Federal-State Land Use Planning Commission for Alaska 1973), spruce-birch forest (Küchler 1966), and moderately high, mixed evergreen and deciduous forest (Spetzman 1963).



Figure 14.—A Picea mariana/Sphagnum spp.-Cladina spp. community. Trees in this stand (no. 208) are 65 years old.

12. Picea mariana/Sphagnum spp.-Cladina spp. community type

Stands of this type are characterized by woodlands or open forests in which black spruce (Picea mariana) dominates the tree canopy; and mosses, especially Sphagnum spp., low shrubs, and lichens dominate the forest floor (fig. 14). Thaw ponds may or may not be present.

Stands typifying this community type occur on valley bottoms or on north-facing slopes where ice-rich permafrost is present and a perched water table is common. A surface horizon of organic material 0.3 m to over 1 m thick overlies loess or valley alluvium. Soils on these sites are cool and moist. Surface soils melt to a depth of 30 cm by late June and 60 cm by August. Excess water from melting frozen soil and precipitation collects in low depressions and thaw ponds or is absorbed by the mounds of Sphagnum spp. which have very high water-holding capacities. The permafrost layer prevents the downward movement of water.

The flora found on these sites can tolerate the cool, moist conditions. Species such as tussock cottongrass, leatherleaf, some sedges, and bog cranberry need the moisture, whereas Sphagnum spp., narrow-leaf Labrador-tea, dwarf arctic birch, diamondleaf willow, crowberry, and cloudberry can tolerate both the coolness and the moisture. Because Sphagnum spp. have the capacity to absorb and retain water, they help create sites where these species thrive. Table 14 gives information on the species with mean frequencies of 50 percent or more.

In 60- to 130-year-old stands, the black spruce trees are 2.5- to 10.0-cm d.b.h., 2-7 m tall, and average 100-600 stems/ha. Older trees have the larger diameters. Saplings average 300 stems/ha and seedlings 8,900 stems/ha. Sites with the most moisture have the fewest trees. Alaska larch may occur but is not common. The forest floor is covered with low shrubs and mosses, although herbs and lichens are common. Mountain-cranberry, narrow-leaf Labrador-tea, bog blueberry, dwarf arctic birch, and crowberry intermix in varying amounts to form the extensive low shrub layer.

Sphagnum spp., with an average cover of 50 percent, is the most important moss, but both Pleurozium schreberi and Polytrichum spp. can be common. Herbs such as cloudberry, sedges, and tussock cottongrass are common to all or most stands of this community type. Lichens, especially Cladina rangiferina and C. arbuscula, grow intermixed with the moss. Litter and rotting logs are quickly incorporated into the moss layer.

Thaw ponds may form where the moss insulating layer is broken by uprooting of trees or soil heavings. Ponds continue to grow in size until the unprotected permafrost melts or the water table drops. In time the ponds fill in or become covered with enough floating vegetation to once again support shrubs and trees.

Stands of this community type burn at least superficially. When this happens, the vegetation reestablishes itself from root suckers, unburned seeds in situ or from numerous patches left untouched by fire.

The Picea mariana/Sphagnum spp.-Cladina spp. community type has been variously named: open Picea mariana/Sphagnum-Cladonia (Neiland and Viereck 1977, Viereck and Dyrness 1980), and black spruce/narrow-leaf Labrador-tea/Sphagnum spp. (see footnote 4). It is also a component of the more general types: black spruce (Lutz 1956), muskeg (Buckley and Libby 1957), and open, low-growing spruce (Viereck and Little 1972). On vegetation maps with scales of 1:2,500,000 and 1:7,500,000, it is a component of the following types: lowland spruce-hardwood forest (Joint Federal-State Land Use Planning Commission for Alaska 1973), black spruce forest and muskeg types (Küchler 1966), and low, mixed evergreen and deciduous forest (Spetzman 1963).

Table 14—Important plant species and litter components of the *Picea mariana*/*Sphagnum* spp.-*Cladina* spp. community type (Type 12) of interior Alaska

Species and litter component	Mature stands 1/			
	Cover 2/	Density 3/	D.b.h. 4/	Frequency 5/
	Percent	Stems/ha	Cm	Percent
Tree layer:				
<i>Picea mariana</i> --				
Mature trees	—	300	5.8-8.1	100
Saplings	—	300	—	100
Seedlings	—	8,900	—	85
Low shrub layer:				
<i>Betula nana</i>	5	—	—	80
<i>Empetrum nigrum</i>	7	—	—	65
<i>Ledum decumbens</i>	11	—	—	65
<i>Vaccinium oxycoccus</i>	2	—	—	55
<i>Vaccinium uliginosum</i>	6	—	—	95
<i>Vaccinium vitis-idaea</i>	9	—	—	100
Herb layer:				
<i>Carex</i> spp.	12	—	—	80
<i>Rubus chamaemorus</i>	7	—	—	100
Mosses:				
<i>Pleurozium schreberi</i>	22	—	—	70
<i>Polytrichum</i> spp.	9	—	—	75
<i>Sphagnum</i> spp.	50	—	—	85
Lichens:				
<i>Cladina arbuscula</i>	4	—	—	60
<i>Cladina rangiferina</i>	4	—	—	60
Litter component:				
Leaves and twigs	13	—	—	100
Dead wood and fallen logs	3	—	—	45

1/ Number of stands sampled: 3; age: 60-130 years; number of species found: 28-36; depth of organic layer: 20-30 cm and over; depth of active thaw layer: 30-120 cm and over.

2/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: $\text{Cover} = \Sigma (\text{mean stand cover value for a species}) \div \text{total number of stands sampled}$. The values given are rounded to the nearest whole number.

3/ The computed or counted number of stems occurring in a given area. It is based on the equation: $\text{Density} = \Sigma (\text{mean stand density value for a species}) \div \text{total number of stands sampled}$. The values given above 200 are rounded to the nearest 100; the values below 100 are rounded to the nearest whole number.

4/ D.b.h. is the diameter of a tree at breast height. The mean stand d.b.h. value for a species is given; when more than 1 stand was sampled, the range of mean values is given.

5/ The percent of plots in which a given species occurs. It is based on the equation: $\text{Frequency} = \Sigma (\text{mean stand frequency value for a species}) \div \text{total number of stands sampled}$. The values given are rounded to the nearest whole number.

Forest Succession

To understand succession, one must first understand fire. Fires vary in size, type, rate and direction of spread, intensity, and duration. Surface fires consume fuel on the forest floor including bases of trees. Crown fires sweep from treetop to treetop and may never reach the ground. Fire can travel up or down tree boles causing a ground fire to become a crown fire and vice versa. Fire can be stationary or move rapidly ahead, change direction or even reverse itself without warning, and can jump to new areas ahead of or behind the main center of flame activity. Because of this, fire burns across the landscape in an irregular and uneven manner. The burned surface may or may not be essentially the same as the preburned surface. The depth to which organic material is consumed is highly variable. Sometimes organic matter is left, and sometimes mineral soil is exposed.

Fire likewise leaves the vegetation it touches in a variety of conditions: unburned, scorched, charred, partially killed, or completely consumed. In general, a severe and long-lasting fire burns more organic matter (including live vegetation), produces more ash, and exposes more mineral soil. Ground surfaces and most snags are left black with carbon, and plant growth is terminated, at least temporarily.

Succession after fire in forest ecosystems in interior Alaska is complex and related to site, fire, climate, the type and age of vegetation present before fire, and the plant species available for sprouting or invasion after fire. Black spruce stands return to black spruce, and white spruce stands eventually return to white spruce. Each site, however, is unique both in its rate of change and composition of species.

This study identified six developmental stages in the revegetation process: (1) newly burned, (2) moss-herb, (3) tall shrub-sapling, (4) dense tree, (5) hardwood or mixed hardwood-spruce, and (6) spruce.

1.—The newly burned stage lasts from the time of fire until the area is again dominated by living plants. It can be as short as 1 month in areas where burns are light or as long as 3–4 years where burns are severe and few plants are available for reinvasion.

Soon after fire, however, things begin to happen. With the next rain charcoal and ash start to mix with the organic and mineral soil layers. The reappearance of plants may be rapid or slow; it is limited by: (a) the presence of underground plant parts with the capacity to sprout, (b) the availability of spores and seed, (c) the presence of suitable seedbed, and (d) favorable climatic and weather conditions. Usually within 2–3 weeks after fire, green plants become visible. The first to appear are shoots at the bases of snags and above buried roots or underground stems which were not killed by the fire. These shoots are soon followed by protonema of mosses, young thalli of liverworts, and seedlings of vascular plants, especially on areas of exposed mineral soil. As the vegetation becomes increasingly prominent, the newly burned stage phases into the moss-herb stage.

2.—The moss-herb stage is characterized by moss, herbs, seedlings of trees and shrubs, and newly fallen litter. It can begin as early as 3 months after fire or as late as 3 years after fire. It will last 3–10 years, or until the shrubs and trees overtop the herb layer.

The first 3–6 years is a time of plant establishment, when seedbeds are most receptive to seed germination and seedling growth. Thereafter, accumulating litter and developing plant cover make seedbeds less available to new seed, and competition between plants usually favors larger plants over younger, smaller seedlings. The established mix of mosses, liverworts, herbs, shrubs, and trees continues to grow in height, canopy cover, and mass, and the species that reproduce vegetatively do so. Rapidly the herb canopy closes. Eventually the taller shrubs and trees will overtop the lower growing plants and the next stage, the tall shrub-sapling stage, will arrive.

This successional trend can be altered in several ways. If seedlings of trees and shrub species are not established, the area will stagnate in the moss-herb stage. Or if the young trees and shrubs are heavily impacted by animals, species can be exterminated, leaving the moss-herb stage intact. Animals and birds can selectively exhaust the seeds, shoots, or stems of preferred species. Grassy areas within a forest may represent areas where tree and shrub seedlings never became established or failed to survive.

3.—If succession continues, the tall shrub-sapling stage develops. This stage is characterized by 1.4- to 7-m tall shrubs and/or saplings. It develops sometime within 3-30 years after fire and lasts about 20 years. Fast growing sucker shoots reach breast height (1.4 m) in 3 years, fast growing seedlings in 5-10 years, and slow growing seedlings in 10-30 years.

As this stage develops, the shrub-sapling canopy gradually closes and leaf litter accumulates on the forest floor; however, before the canopy closes, the herb layer, developed in the previous stage, continues to expand. After the canopy closes, the herb layer, in general, wanes.

In time, the saplings grow into trees and overtop the shrubs. When this happens, the tall shrub-sapling stage grades into the dense tree stage.

Many stands of the tall shrub-sapling stage are utilized extensively by moose and snowshoe hares for browse, especially in winter, and for shelter. They prefer young, small-diameter stems of quaking aspen, certain willow species, Alaska larch, and paper birch but will browse other species. Snowshoe hares can reach twigs 60 cm above the snow line; moose can reach higher.

Moderate browsing at this stage appears to stimulate shrub productivity (Wolff 1978). Sustained intensive browsing, as on the Kenai Peninsula, perpetuates the shrub stage. On the 20-year-old Kenai Lake burn, the tall shrubs and trees are clipped by moose each winter at a height of 50-100 cm above the ground, and each summer the plants send up new shoots; in the adjacent moose enclosure, plants of the same postfire age are more than 6 m tall. The more common pattern is for browsing to continue only until the shrubs have grown too tall or the stems too large in diameter for the animals to reach directly or by bending them. This usually happens within 15-20 years after fire. This temporary impact does not stop succession.

4.—The dense tree stage is reached when trees are at least 2.5-cm d.b.h., 4-8 m tall, and overtop the shrubs. This stage is first attained 15-40 years after fire, depending on growth patterns of tree species. Quaking aspen requires 15-30 years, paper birch 20-30 years (Gregory and Haack 1965), and white spruce 15-30 years (Farr 1967). Black spruce grows even more slowly. As it continues to develop, the faster growing trees become dominant, the slower growing trees the subdominates, and the unsuccessful die. Stands of this stage are usually dense.

The dense tree stage is transitional, between the early stages dominated by herbs and shrubs and the later stages dominated by trees. Species characteristic of earlier stages—Ceratodon purpureus, Marchantia polymorpha, fireweed, and most willows—have disappeared, some entirely, while species characteristic of later successional stages—Pleurozium schreberi, and alder—are increasing, sometimes rapidly. Other important changes are also occurring. Cladonia spp. and Cladina spp. have appeared in important amounts. The understory vegetation is restricted for the most part to shade-tolerant species that can grow beneath the now-closed tree canopy. And fuels, both dead and living, occur in sufficient quantities to make stands in this developmental stage very flammable. In fact, it is

not uncommon for stands in the dense tree stage to be destroyed or at least impacted by fire. When fire occurs, forward succession is terminated and the successional process starts over. If fire does not occur, this stage continues until the hardwood trees are mature and the next, or hardwood stage, has arrived. If no hardwoods are present, however, the dense tree stage passes directly into the spruce stage.

5.—The hardwood stage is characterized by well-developed hardwoods such as quaking aspen, paper birch, and balsam poplar in either pure or mixed stands. Spruce may occur as understory, subdominant, codominant, or occasionally as the dominant tree. Stands of this stage are composed of 50- to 150-year-old trees. The stage continues until the hardwood trees die. Quaking aspen are the shortest lived, many dying at 70-80 years of age, paper birch live 120-150 years, and balsam poplar 120-200 years.

Beneath the trees, various combinations of shrubs, herbs, and mosses exist. Species which tend to increase in cover and/or density as the stand ages do well, whereas opportunistic species are locally abundant to rare. As the stage advances, spruce and moss become more important. Lichens are less common than in the previous stage.

The larger the hardwood component, the more fire resistant the stands are; however, all will burn. In fact, many stands burn before the trees are 100 years old. Succession then starts anew. If stands do not burn, they continue to age and eventually develop into the next stage, the spruce stage.

6.—The spruce stage is characterized by closed- to open-canopied stands of spruce in which occasional hardwoods may remain. Most of the stands are 100-200 years old. The understory is a mixture of tall shrubs, low shrubs, herbs, mosses, and lichens. Feathermosses reach their best development in this stage.

This is the oldest stage and occurs in interior Alaska where disturbance, such as fire, has been minimal to nonexistent. Since fire burns extensive areas each year, few areas have escaped its impact during the last 300 years. Thus, stands representing the old, pure spruce stands are less numerous than those representing the younger stages.

The maximum duration of this stage is academic, since the oldest spruce trees known in interior Alaska are just under 300 years old (see footnote 5). Enough reproduction exists within most stands to maintain this stage, however, until fire or other disturbances destroy them.

This is the general pattern of postfire succession. Next are examples of what each developmental stage can look like, first on white spruce sites, and then on mesic black spruce sites. Sample size is small, however, and generalizations for the entire taiga are not implied.

Stages on White Spruce Sites

1.—The newly burned stage (0-1 year after fire) is a time of initial impact and recovery. Ground fires consume or damage vegetation throughout most of the burned areas. Crown fires are less common. Burned sites are dominated by standing dead trees and an expanse of charred ground and ash. Except in unburned pockets, the preburn ground vegetation has been killed and mostly consumed. Trees that have been stem-scorched frequently retain their green leaves. It is initially difficult to determine whether they are dead or alive; most will die.

Within weeks of the fire, growing vegetation is again apparent. The first to be visible are new shoots of prickly rose, high bushcranberry, and willow, which occur near the remains of burned shrubs. Sucker shoots of quaking aspen, and seedlings of fireweed, quaking aspen, and paper birch soon follow. White spruce seedlings rarely appear.



Figure 15.—Newly burned stage on white spruce sites. This stand (BC 4L-4H) is 2 weeks postfire in age. Light colored areas on the forest floor are ash in places where the burn was severe. Adjacent areas with young sucker shoots and forest litter are places where the burn was less severe.

White spruce trees in interior Alaska produce viable seed crops on an irregular basis. Abundant seed is produced once every 10 years (Zasada and Viereck 1970). Small quantities of seed may be produced locally in intervening years. If seeds reach recently burned ground, seedlings will develop. More often, white spruce seed is not available so the species is absent from the burned area.

Figure 15 and tables 15 and 21, p. 56 and 68, show what occurred on sampled sites in the newly burned stage. Quaking aspen, prickly rose, high bushcranberry, and fireweed occurred in all stands. Paper birch, willow, American red raspberry, field horsetail, reed-grass, and northern bedstraw occurred in most stands but in lesser amounts.

By the end of the first growing season, the shoots were 2–50 cm tall and the seedlings 1–10 cm in height. Tall shrubs and tree seedlings, including suckers, averaged the following densities: prickly rose 45,462 stems/ha; high bushcranberry 37,562; quaking aspen 28,312; paper birch 1,688; willow 5,250; and American red raspberry 562. The leading herb, fireweed, covered 7 percent of the area. There were small amounts of new litter on the forest floor. Thus vegetation began to cover areas that were initially charred ground and the next, or moss-herb, stage was near.

2.—The moss-herb stage (1–5 years after fire) is a time of continued introduction and expansion of species. In addition to the species found in the newly burned stage, others were also found: Bebb willow, twin-flower, mountain-cranberry, tall bluebell, bluntleaved sandwort, Ceratodon purpureus, Polytrichum spp., and Marchantia polymorpha (fig. 16; tables 16 and 21, p. 58 and 68).

Four years after the fire, the vegetation was dominated by the oldest species (quaking aspen, prickly rose, various willows, and fireweed), one additional species (Ceratodon purpureus), and litter. Quaking aspen and paper birch each averaged about 30,000 stems/ha (both sucker shoots and seedlings) and were 1–2 m tall. Tall shrubs averaged 9,969 stems/ha for prickly rose; 6,906 for high bushcranberry; and 2,547 for willow (mostly Bebb willow). Herbs, on the average, covered 30 percent of the ground; one species, fireweed, accounted for 14 percent or almost half. Mosses, on the average, covered 30 percent of the area; one species, Ceratodon purpureus, accounted for most (16 percent). This rapidly expanding moss forms extensive patches, especially in areas of exposed mineral soil. Deadfall litter covered, on the average, 62 percent of the area. As the litter accumulates, it forms an ever-thickening layer of organic material in various stages of decomposition. The layer in this stage averaged 3 cm in depth.

3.—The tall shrub-sapling stage (3–30 years after fire) is a period of domination by tall shrubs and/or saplings in the overstory, and herbs, tree seedlings, and litter below (fig. 17). The vegetation continues from the moss-herb stage. Introduction of new species may continue for a short time but essentially stops by the end of this stage. Mosses and lichens exist but are not important components.

Fifteen years after the fire (a mean age for this stage), the overstory saplings (mostly quaking aspen) averaged 3,256 stems/ha; willows (mostly Bebb and grayleaf) 21,737; and other tall shrubs (mostly prickly rose and high bushcranberry in equal amounts) 75,889 (tables 17 and 21, p. 60 and 68). The saplings and willows were 2–5 cm tall and the prickly rose and high bushcranberry 1–2 m tall. In the understory, seedlings and sucker shoots (mostly quaking aspen) averaged 31,792 stems/ha; herbs (mostly fireweed, reedgrass, and field horsetail) covered on the average, 45 percent of the area; and low shrubs (no dominating species) 6 percent. On the forest floor, litter (mostly deadfall leaves) averaged 90-percent cover; mosses (mostly Ceratodon purpureus) 8 percent; while lichens (mostly Peltigera spp.) averaged 2 percent. The organic layer averaged 8 cm in depth. The plants grow taller as the organic layer grows thicker. With time the saplings will overtop the shrubs and become trees and the next stage will arrive.

Figure 17.—Tall shrub-sapling stage on white spruce sites. This 3-year-old community has 26,000 quaking aspen saplings and 67,000 tall shrub stems per hectare.



Figure 16.—Moss-herb stage on white spruce sites. The site of this 1-year-old community had been severely to moderately burned. Fireweed and field horsetail dominate on the severely burned areas; those herbs plus quaking aspen seedlings dominate areas moderately burned.





Figure 18.—Dense tree stage on white spruce sites. This stand (no. 150) has 1,645 trees/ha.

4.—The dense tree stage (26 to 45 years after fire) is a period of dominance by young trees in the overstory, and high bushcranberry, prickly rose, twin-flower, mountain-cranberry, Labrador-tea, and litter below (fig. 18). Cladonia spp. (lichens), never very extensive, are best developed at this time, and feather-mosses, especially Pleurozium schreberi, are now established. Willows, herbs, and seral mosses are no longer important components.

Dominant trees in sampled stands averaged 36 years in age. Overstory trees (mostly paper birch and quaking aspen) averaged 2,319 stems/ha, 8.4- to 11.1-cm d.b.h., and 6-10 m tall (tables 18 and 21, p. 62 and 68). Understory tall shrubs (mostly high bushcranberry and prickly rose) averaged 16,075, willows (mostly Bebb) 800, and seedlings (mostly hardwoods) 1,650 stems/ha. Low shrubs and

herbs (no dominant species) covered, on the average, 14 and 10 percent, respectively, of the forest floor. Leaf litter was found on 93 percent of the ground; mosses, mostly Pleurozium schreberi and Polytrichum spp., on 14 percent; while lichens (Cladonia spp. and Peltigera spp. in equal amounts) occurred on 2 percent of the ground. The organic layer remained about 8 cm thick.

As these stands age, the dense trees will undergo self-thinning and the surviving trees will increase in height and diameter. The next stage, the hardwood stage, is near.

5.—The hardwood stage (46-150 years after fire) is characterized by well-developed stands of quaking aspen, paper birch, or mixtures of hardwood and hardwood-white spruce (see figs. 3, 4, and 5). High bushcranberry, prickly rose, twin-flower, and field horsetail dominate the understory, while leaf litter and Hylocomium splendens dominate the forest floor. Willows, mosses, and lichens are not important components. Paper birch trees tend to outlive quaking aspen trees by 30 to 50 years. Towards the end of this stage, the stands are mostly paper birch and/or mixtures of paper birch and white spruce.

The stands studied in this stage averaged 87 years in age. Of the 909 trees/ha, one-half were quaking aspen, one-third paper birch, and one-sixth white spruce (tables 19 and 21, p. 64 and 68). The dominant trees averaged 18.5- to 20.8-cm d.b.h. and 17-26 m in height. Of the 58,170 stems/ha of tall shrub, 65 percent were high bushcranberry, 30 percent prickly rose, and 4 percent American green alder. Low shrubs covered, on the average, 7 percent of the area and were half twin-flower and one-half mountain-cranberry and Labrador-tea. Herbs covered 7 percent of the ground. Field horsetail, the most abundant herb, accounted for half this amount. Hylocomium splendens formed 6 percent or half the total moss cover. Leaf litter covered, on

the average, 86 percent of the area, while the organic layer averaged 11 cm in depth. Numerous tree seedlings were found, especially on mineral soil exposed by uprooted and fallen trees. Most of these (20,761 per hectare) were paper birch. There was little evidence, however, these seedlings would survive for long.

This stage will end as the hardwood trees stagnate and die, leaving the codominant and/or understory white spruce to form the overstory canopy.

6.--The spruce stage (150-300+ years after fire) occurs after the shorter lived plants have failed to replace themselves (see figs. 6 and 7). The overstory canopy of white spruce is open to closed. A few hardwood trees, relics of an earlier stage, may occur in the beginning years but eventually die. Prickly rose and high bush-cranberry usually dominate the tall shrub layer, though they may be entirely displaced by thickets of American green alder. Twin-flower and field horsetail dominate the understory. Hylocomium splendens blankets the forest floor, covering litter, fallen logs, and slow growing vegetation. Willows are absent and lichens are present only in minimal amounts. This stage will develop earlier than 150 years after fire if the hardwoods die when younger or if no hardwoods are present in the dense tree stage.

As stands in the spruce stage age, three changes occur: (1) the trees increase in diameter but stagnate in height, (2) the moss layer increases in extent and depth, and (3) American green alder appears to increase in density.

The stands studied averaged 170 years in age. Trees (mostly white spruce) averaged 566 stems/ha, 19.1-cm d.b.h., and 30 m in height (tables 20 and 21, p. 66 and 68). The 21,781 stems/ha of tall shrubs were 65 percent prickly rose, 23 percent high bush-cranberry, and 12 percent American green alder. Twin-flower covered 6 percent of the area and accounted for most of the low shrub layer. Field horsetail covered 4 percent of the area, while Geocalyon lividum covered 3 percent. Together they accounted for 70 percent of the herb layer. In the moss layer, Hylocomium splendens covered, on the average, 61 percent and Pleurozium schreberi, 5 percent. Litter was visible on 26 percent of the ground, and the litter-organic layer averaged 12 cm in depth.

No one knows how long this stage might last in interior Alaska. The oldest known trees are 300 years old. Many of these are still healthy and free of center rot. At current rates, fire, landclearing, and logging will terminate or impact most of these white spruce stands in the near future.

Tables 15-20 are grouped together on p. 56-67 to aid the reader in following the succession of common species on white spruce sites through the six developmental stages. A summary appears in table 21, p. 68.

Table 15—Quantitative description of the newly burned stage of plant succession on white spruce sites in the talga of Interior Alaska, by dominant plant species and litter component 1/

Quantitative description of the newly burned stage								
Species and litter component <u>2/</u>	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Tree layer:								
<u>Betula papyrifera</u> —								
Mature trees	<u>7/</u> (14)	(16)	—	—	(69)	(86)	(6.7)	(3.8)
Saplings	0	0	—	—	0	0	—	—
Seedlings	12	25	—	—	1,688	3,375	—	—
<u>Picea glauca</u> —								
Mature trees	(19)	(38)	—	—	(225)	(450)	(17.5)	(0)
Saplings	0	0	—	—	0	0	—	—
Seedlings	0	0	—	—	0	0	—	—
<u>Populus balsamifera</u> —								
Mature trees	(15)	(30)	—	—	(294)	(589)	(8.2)	(0)
Saplings	2	5	—	—	2	4	2.0	0
Seedlings	0	0	—	—	0	0	—	—
<u>Populus tremuloides</u> —								
Mature trees	(59)	(42)	—	—	(377)	(389)	(18.8)	(6.3)
Saplings	0	0	—	—	0	0	—	—
Seedlings	55	33	—	—	28,312	47,551	—	—
Tall shrub layer:								
<u>Alnus crispa</u> <u>8/</u>	0	0	—	—	0	0	—	—
<u>Rosa acicularis</u>	88	25	—	—	45,562	23,740	—	—
<u>Rubus idaeus</u>	10	14	—	—	562	966	—	—
<u>Salix arbusculoides</u>	0	0	—	—	0	0	—	—
<u>Salix bebbiana</u>	0	0	—	—	0	0	—	—
<u>Salix glauca</u>	0	0	—	—	0	0	—	—
<u>Other Salix spp.</u>	15	17	—	—	5,250	5,990	—	—
<u>Viburnum edule</u>	78	22	—	—	37,562	37,220	—	—
Low shrub layer:								
<u>Ledum groenlandicum</u>	0	0	0	0	—	—	—	—
<u>Linnaea borealis</u>	2	5	<u>9/</u>	<u>9/</u>	—	—	—	—
<u>Vaccinium vitis-idaea</u>	0	0	0	0	—	—	—	—
Herb layer:								
<u>Calamagrostis</u> spp.	22	29	1	1	—	—	—	—
<u>Cornus canadensis</u>	20	23	<u>9/</u>	<u>9/</u>	—	—	—	—
<u>Epilobium angustifolium</u>	80	40	7	5	—	—	—	—
<u>Equisetum arvense</u> <u>10/</u>	20	40	1	2	—	—	—	—
<u>Equisetum scirpoides</u>	0	0	0	0	—	—	—	—
<u>Galium boreale</u>	65	40	1	1	—	—	—	—
<u>Geocaulon lividum</u>	0	0	0	0	—	—	—	—
<u>Lycopodium annotinum</u> <u>11/</u>	2	5	<u>9/</u>	<u>9/</u>	—	—	—	—
<u>Mertensia paniculata</u>	28	22	<u>9/</u>	<u>9/</u>	—	—	—	—
<u>Moehringia lateriflora</u>	0	0	0	0	—	—	—	—
<u>Pyrola asarifolia</u> <u>12/</u>	0	0	0	0	—	—	—	—
<u>Pyrola secunda</u>	0	0	0	0	—	—	—	—

See footnotes at end of table.

Table 15—Quantitative description of the newly burned stage of plant succession on white spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/ (continued)

Species and litter component 2/	Quantitative description of the newly burned stage							
	Frequency 3/		Cover 4/		Density 5/		D.b.h. 6/	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Mosses:								
<u>Ceratodon purpureus</u>	0	0	0	0	—	—	—	—
<u>Dicranum spp.</u>	0	0	0	0	—	—	—	—
<u>Drepanocladus uncinatus</u>	0	0	0	0	—	—	—	—
<u>Hylocomium splendens</u>	0	0	0	0	—	—	—	—
<u>Marchantia polymorpha</u>	0	0	0	0	—	—	—	—
<u>Pleurozium schreberi</u>	0	0	0	0	—	—	—	—
<u>Polytrichum spp.</u>	0	0	0	0	—	—	—	—
Lichens:								
<u>Cladonia spp. 13/</u>	0	0	0	0	—	—	—	—
<u>Peltigera spp.</u>	0	0	0	0	—	—	—	—
Litter component:								
Charred material	100	0	96	4	—	—	—	—
Leaves and twigs	100	0	15	8	—	—	—	—
Dead wood and fallen logs	100	0	8	1	—	—	—	—

1/ Number of stands sampled: 4; age: mean 6 months after fire (standard deviation 7); number of species found: mean 12 (standard deviation 3); depth of organic layer: no data available.

2/ Only species with a frequency of at least 30 percent in at least 1 stand are listed in tables 15–20. Not all of those species occur in every stage of succession; all are listed for each stage, however, to enhance comparison of their development.

3/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

4/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

5/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

6/ D.b.h. is the diameter of a tree at breast height. The values given are for trees 2.5 cm in d.b.h. or larger and are based on the equation: D.b.h. = Σ (mean d.b.h. values for a species in a stand) \div total number of stands sampled.

7/ Numbers in parentheses indicate the number of trees that originated before the fire.

8/ Includes Alnus tenuifolia from river-bottom sites.

9/ Less than 0.5 percent.

10/ Includes Equisetum pratense.

11/ Includes Lycopodium clavatum.

12/ Includes Pyrola chlorantha.

13/ Includes Cladina spp.

Table 16—Quantitative description of the moss-herb stage of plant succession on white spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/

Quantitative description of the moss-herb stage								
Species and litter component <u>2/</u>	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Tree layer:								
<u>Betula papyrifera</u> —								
Mature trees	<u>7/</u> (26)	(37)	—	—	(126)	(309)	(11.3)	(7.6)
Saplings	1	2	—	—	8/	8/	0.1	0
Seedlings	34	42	—	—	32,969	75,635	—	—
<u>Picea glauca</u> —								
Mature trees	(1)	(2)	—	—	(2)	(4)	(7.5)	(0)
Saplings	0	0	—	—	0	0	—	—
Seedlings	4	12	—	—	109	309	—	—
<u>Populus balsamifera</u> —								
Mature trees	(1)	(4)	—	—	(3)	(8)	(15.7)	(0)
Saplings	10	28	—	—	5	14	0.8	0
Seedlings	1	2	—	—	31	58	—	—
<u>Populus tremuloides</u> —								
Mature trees	(25)	(35)	—	—	(71)	(174)	(12.7)	(8.5)
Saplings	61	51	—	—	2,412	4,194	0.9	0.4
Seedlings	78	27	—	—	30,000	29,509	—	—
Tall shrub layer:								
<u>Alnus crispa</u> <u>9/</u>	2	5	—	—	109	309	—	—
<u>Rosa acicularis</u>	40	37	—	—	9,969	19,305	—	—
<u>Rubus idaeus</u>	4	10	—	—	359	967	—	—
<u>Salix arbusculoides</u>	0	0	—	—	0	0	—	—
<u>Salix bebbiana</u>	28	34	—	—	2,109	1,952	—	—
<u>Salix glauca</u>	0	0	—	—	0	0	—	—
Other <u>Salix</u> spp.	11	17	—	—	438	785	—	—
<u>Viburnum edule</u>	21	38	—	—	6,906	18,048	—	—
Low shrub layer:								
<u>Ledum groenlandicum</u>	2	4	2	3	—	—	—	—
<u>Linnaea borealis</u>	26	33	2	4	—	—	—	—
<u>Vaccinium vitis-idaea</u>	20	35	2	4	—	—	—	—
Herb layer:								
<u>Calamagrostis</u> spp.	37	36	4	8	—	—	—	—
<u>Cornus canadensis</u>	12	32	1	3	—	—	—	—
<u>Epilobium angustifolium</u>	91	19	14	15	—	—	—	—
<u>Equisetum arvense</u> <u>10/</u>	32	43	4	8	—	—	—	—
<u>Equisetum scirpoides</u>	26	43	1	2	—	—	—	—
<u>Galium boreale</u>	8	21	8/	1	—	—	—	—
<u>Geocaulon lividum</u>	4	7	8/	8/	—	—	—	—
<u>Lycopodium annotinum</u> <u>11/</u>	7	9	1	3	—	—	—	—
<u>Mertensia paniculata</u>	12	15	8/	8/	—	—	—	—
<u>Moehringia lateriflora</u>	21	34	1	1	—	—	—	—
<u>Pyrola asarifolia</u> <u>12/</u>	0	0	0	0	—	—	—	—
<u>Pyrola secunda</u>	18	35	1	2	—	—	—	—

See footnotes at end of table.

Table 16—Quantitative description of the moss-herb stage of plant succession on white spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/ (continued)

Species and litter component <u>2/</u>	Quantitative description of the moss-herb stage							
	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----		----- Stems/ha -----		----- Centimeters -----			
Mosses:								
<u>Ceratodon purpureus</u>	76	36	16	16	—	—	—	—
<u>Dicranum</u> spp.	0	0	0	0	—	—	—	—
<u>Drepanocladus uncinatus</u>	7	14	8/	8/	—	—	—	—
<u>Hylocomium splendens</u>	5	9	8/	8/	—	—	—	—
<u>Marchantia polymorpha</u>	15	21	1	2	—	—	—	—
<u>Pleurozium schreberi</u>	13	24	8/	8/	—	—	—	—
<u>Polytrichum</u> spp.	54	38	4	6	—	—	—	—
Lichens:								
<u>Cladonia</u> spp. <u>13/</u>	6	12	8/	8/	—	—	—	—
<u>Peltigera</u> spp.	23	39	2	3	—	—	—	—
Litter component:								
Charred material	42	46	15	29	—	—	—	—
Leaves and twigs	75	46	62	40	—	—	—	—
Dead wood and fallen logs	84	35	7	4	—	—	—	—

1/ Number of stands sampled: 8; age: mean 4 years after fire (standard deviation 2); number of species found: mean 20 (standard deviation 6); depth of organic layer: mean 3 cm (standard deviation 1).

2/ Only species with a frequency of at least 30 percent in at least 1 stand are listed in tables 15–20. Not all of those species occur in every stage of succession; all are listed for each stage, however, to enhance comparison of their development.

3/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

4/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

5/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density, value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

6/ D.b.h. is the diameter of a tree at breast height. The values given are for trees 2.5 cm in d.b.h. or larger and are based on the equation: D.b.h. = Σ (mean d.b.h. values for a species in a stand) \div total number of stands sampled.

7/ Numbers in parentheses indicate the number of trees that originated before the fire.

8/ Less than 0.5 percent.

9/ Includes *Alnus tenuifolia* from river-bottom sites.

10/ Includes *Equisetum pratense*.

11/ Includes *Lycopodium clavatum*.

12/ Includes *Pyrola chlorantha*.

13/ Includes *Cladina* spp.

Table 17—Quantitative description of the tall shrub-sapling stage of plant succession on white spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/

Quantitative description of the tall shrub-sapling								
Species and litter component <u>2/</u>	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Tree layer:								
<u>Betula papyrifera</u> —								
Mature trees	33	33	—	—	27	37	3.7	0.6
Saplings	51	44	—	—	109	143	1.2	0.5
Seedlings	28	23	—	—	4,250	4,058	—	—
<u>Picea glauca</u> —								
Mature trees	10	22	—	—	8	16	4.1	0.4
Saplings	12	26	—	—	28	48	1.6	0.2
Seedlings	38	38	—	—	4,583	6,096	—	—
<u>Populus balsamifera</u> —								
Mature trees	7	20	—	—	5	13	3.4	0.2
Saplings	12	19	—	—	116	279	0.9	0.1
Seedlings	13	24	—	—	3,486	9,678	—	—
<u>Populus tremuloides</u> —								
Mature trees	43	45	—	—	83	174	5.2	1.9
Saplings	55	46	—	—	3,003	7,001	1.4	0.4
Seedlings	48	46	—	—	19,194	30,210	—	—
Tall shrubs:								
<u>Alnus crispa</u> <u>7/</u>	9	11	—	—	958	1,248	—	—
<u>Rosa acicularis</u>	60	39	—	—	38,222	61,931	—	—
<u>Rubus idaeus</u>	19	35	—	—	3,403	6,708	—	—
<u>Salix arbusculoides</u>	19	30	—	—	1,903	3,805	—	—
<u>Salix bebbiana</u>	24	38	—	—	11,028	21,873	—	—
<u>Salix glauca</u>	27	37	—	—	7,306	12,866	—	—
<u>Other Salix spp.</u>	7	11	—	—	1,500	3,057	—	—
<u>Viburnum edule</u>	30	38	—	—	33,222	59,051	—	—
Low shrubs:								
<u>Ledum groenlandicum</u>	3	8	<u>8/</u>	<u>8/</u>	—	—	—	—
<u>Linnaea borealis</u>	22	24	<u>1</u>	<u>2</u>	—	—	—	—
<u>Vaccinium vitis-idaea</u>	12	30	<u>8/</u>	<u>1</u>	—	—	—	—
Herbs:								
<u>Calamagrostis spp.</u>	64	16	8	8	—	—	—	—
<u>Cornus canadensis</u>	31	44	12	22	—	—	—	—
<u>Epilobium angustifolium</u>	80	26	7	9	—	—	—	—
<u>Equisetum arvense</u> <u>9/</u>	57	36	5	6	—	—	—	—
<u>Equisetum scirpoides</u>	28	34	2	4	—	—	—	—
<u>Galium boreale</u>	31	40	4	7	—	—	—	—
<u>Geocaulon lividum</u>	9	20	<u>8/</u>	<u>8/</u>	—	—	—	—
<u>Lycopodium annotinum</u> <u>10/</u>	1	3	<u>8/</u>	<u>8/</u>	—	—	—	—
<u>Mertensia paniculata</u>	24	20	<u>1</u>	<u>1</u>	—	—	—	—
<u>Moehringia lateriflora</u>	17	15	<u>8/</u>	<u>1</u>	—	—	—	—
<u>Pyrola asarifolia</u> <u>11/</u>	6	10	<u>8/</u>	<u>8/</u>	—	—	—	—
<u>Pyrola secunda</u>	14	17	<u>8/</u>	<u>8/</u>	—	—	—	—

See footnotes at end of table.

Table 17—Quantitative description of the tall shrub-sapling stage of plant succession on white spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/ (continued)

Species and litter component <u>2/</u>	Quantitative description of the tall shrub-sapling							
	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Mosses:								
<u>Ceratodon purpureus</u>	60	31	6	7	—	—	—	—
<u>Dicranum spp.</u>	0	0	0	0	—	—	—	—
<u>Drepanocladus uncinatus</u>	6	13	8/	8/	—	—	—	—
<u>Hylocomium splendens</u>	4	8	8/	8/	—	—	—	—
<u>Marchantia polymorpha</u>	0	0	0	0	—	—	—	—
<u>Pleurozium schreberi</u>	8	11	8/	8/	—	—	—	—
<u>Polytrichum spp.</u>	8	16	1	1	—	—	—	—
Lichens:								
<u>Cladonia spp. <u>12/</u></u>	9	12	8/	8/	—	—	—	—
<u>Peltigera spp.</u>	33	36	4	8	—	—	—	—
Litter component:								
Charred material	7	16	1	1	—	—	—	—
Leaves and twigs	99	2	81	19	—	—	—	—
Dead wood and fallen logs	87	17	8	4	—	—	—	—

1/ Number of stands sampled: 9; age: mean 15 years after fire (standard deviation 8); number of species found: mean 30 (standard deviation 11); depth of organic layer: mean 8 cm (standard deviation 6).

2/ Only species with a frequency of at least 30 percent in at least 1 stand are listed in tables 15-20. Not all of those species occur in every stage of succession; all are listed for each stage, however, to enhance comparison of their development.

3/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

4/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

5/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

6/ D.b.h. is the diameter of a tree at breast height. The values given are for trees 2.5 cm in d.b.h. or larger and are based on the equation: D.b.h. = Σ (mean d.b.h. values for a species in a stand) \div total number of stands sampled.

7/ Includes Alnus tenuifolia from river-bottom sites.

8/ Less than 0.5 percent.

9/ Includes Equisetum pratense.

10/ Includes Lycopodium clavatum.

11/ Includes Pyrola chlorantha.

12/ Includes Cladina spp.

Table 18—Quantitative description of the dense tree stage of plant succession on white spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/

Species and litter component 2/	Quantitative description of the dense tree stage							
	Frequency 3/		Cover 4/		Density 5/		D.b.h. 6/	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Tree layer:								
<u>Betula papyrifera</u> —								
Mature trees	84	16	—	—	1,337	810	11.1	4.4
Saplings	62	21	—	—	41	66	1.9	0.3
Seedlings	9	7	—	—	650	1,044	—	—
<u>Picea glauca</u> —								
Mature trees	22	33	—	—	238	454	8.4	2.2
Saplings	26	29	—	—	9	9	1.8	0.5
Seedlings	4	4	—	—	100	104	—	—
<u>Populus balsamifera</u> —								
Mature trees	0	0	—	—	0	0	—	—
Saplings	0	0	—	—	0	0	—	—
Seedlings	2	3	—	—	200	381	—	—
<u>Populus tremuloides</u> —								
Mature trees	44	36	—	—	718	1,027	8.8	2.2
Saplings	10	17	—	—	2	4	1.5	0.1
Seedlings	11	15	—	—	675	1,088	—	—
Tall shrubs:								
<u>Alnus crispa</u> 7/	7	10	—	—	700	962	—	—
<u>Rosa acicularis</u>	57	30	—	—	5,975	3,542	—	—
<u>Rubus idaeus</u>	8	15	—	—	225	437	—	—
<u>Salix arbusculoides</u>	0	0	—	—	0	0	—	—
<u>Salix bebbiana</u>	13	18	—	—	800	1,304	—	—
<u>Salix glauca</u>	0	0	—	—	0	0	—	—
Other <u>Salix</u> spp.	20	0	—	—	25	56	—	—
<u>Viburnum edule</u>	36	33	—	—	9,175	8,825	—	—
Low shrubs:								
<u>Ledum groenlandicum</u>	22	31	3	3	—	—	—	—
<u>Linnaea borealis</u>	43	29	3	4	—	—	—	—
<u>Vaccinium vitis-idaea</u>	27	42	4	7	—	—	—	—
Herbs:								
<u>Calamagrostis</u> spp.	52	31	3	5	—	—	—	—
<u>Cornus canadensis</u>	35	32	1	1	—	—	—	—
<u>Epilobium angustifolium</u>	38	34	1	2	—	—	—	—
<u>Equisetum arvense</u> 8/	41	44	2	3	—	—	—	—
<u>Equisetum scirpoides</u>	14	26	9/	9/	—	—	—	—
<u>Galium boreale</u>	12	17	9/	9/	—	—	—	—
<u>Geocaulon lividum</u>	0	0	0	0	—	—	—	—
<u>Lycopodium annotinum</u> 10/	5	9	9/	1	—	—	—	—
<u>Mertensia paniculata</u>	12	18	9/	9/	—	—	—	—
<u>Moehringia lateriflora</u>	17	23	9/	9/	—	—	—	—
<u>Pyrola asarifolia</u> 11/	0	0	0	0	—	—	—	—
<u>Pyrola secunda</u>	2	3	9/	9/	—	—	—	—

See footnotes at end of table.

Table 18—Quantitative description of the dense tree stage of plant succession on white spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/ (continued)

Species and litter component 2/	Quantitative description of the dense tree stage							
	Frequency 3/		Cover 4/		Density 5/		D.b.h. 6/	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Mosses:								
<u>Ceratodon purpureus</u>	8	11	9/	9/	—	—	—	—
<u>Dicranum spp.</u>	16	13	1	1	—	—	—	—
<u>Drepanocladus uncinatus</u>	19	25	9/	9/	—	—	—	—
<u>Hylocomium splendens</u>	7	10	3	6	—	—	—	—
<u>Marchantia polymorpha</u>	0	0	0	0	—	—	—	—
<u>Pleurozium schreberi</u>	48	20	5	5	—	—	—	—
<u>Polytrichum spp.</u>	34	32	4	8	—	—	—	—
Lichens:								
<u>Cladonia spp. 12/</u>	32	30	1	1	—	—	—	—
<u>Peltigera spp.</u>	13	14	1	1	—	—	—	—
Litter component:								
Charred material	1	2	9/	9/	—	—	—	—
Leaves and twigs	100	0	88	7	—	—	—	—
Dead wood and fallen logs	69	19	5	1	—	—	—	—

1/ Number of stands sampled: 5; age: mean 36 years after fire (standard deviation 7); number of species found: mean 29 (standard deviation 4); depth of organic layer: mean 8 cm (standard deviation 3).

2/ Only species with a frequency of at least 30 percent in at least 1 stand are listed in tables 15–20. Not all of those species occur in every stage of succession; all are listed for each stage, however, to enhance comparison of their development.

3/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

4/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

5/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

6/ D.b.h. is the diameter of a tree at breast height. The values given are for trees 2.5 cm in d.b.h. or larger and are based on the equation: D.b.h. = Σ (mean d.b.h. values for a species in a stand) \div total number of stands sampled.

7/ Includes Alnus tenuifolia from river-bottom sites.

8/ Includes Equisetum pratense.

9/ Less than 0.5 percent.

10/ Includes Lycopodium clavatum.

11/ Includes Pyrola chlorantha.

12/ Includes Cladina spp.

Table 19—Quantitative description of the hardwood stage of plant succession on white spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/

Quantitative description of the hardwood stage								
Species and litter component <u>2/</u>	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
----- Percent -----			Stems/ha			Centimeters		
Tree layer:								
<u>Betula papyrifera</u> —								
Mature trees	56	45	—	—	317	342	18.5	7.8
Saplings	8	15	—	—	3	3	2.0	0.4
Seedlings	6	11	—	—	20,761	67,867	—	—
<u>Picea glauca</u> —								
Mature trees	26	29	—	—	102	200	18.6	7.2
Saplings	15	28	—	—	6	9	1.4	0.6
Seedlings	2	5	—	—	227	578	—	—
<u>Populus balsamifera</u> —								
Mature trees	1	3	—	—	3	10	17.5	10.0
Saplings	0	0	—	—	0	0	—	—
Seedlings	1	3	—	—	57	188	—	—
<u>Populus tremuloides</u> —								
Mature trees	46	51	—	—	483	582	20.8	6.5
Saplings	9	30	—	—	44	147	0.4	0
Seedlings	11	16	—	—	1,443	2,658	—	—
Tall shrubs:								
<u>Alnus crispa</u> <u>7/</u>	16	16	—	—	2,443	3,231	—	—
<u>Rosa acicularis</u>	75	36	—	—	17,727	16,148	—	—
<u>Rubus idaeus</u>	0	0	—	—	0	0	—	—
<u>Salix arbusculoides</u>	4	12	—	—	272	904	—	—
<u>Salix bebbiana</u>	6	14	—	—	375	835	—	—
<u>Salix glauca</u>	0	0	—	—	0	0	—	—
Other <u>Salix</u> spp.	0	0	—	—	0	0	—	—
<u>Viburnum edule</u>	55	50	—	—	38,000	61,253	—	—
Low shrubs:								
<u>Ledum groenlandicum</u>	7	10	1	1	—	—	—	—
<u>Linnaea borealis</u>	47	29	3	6	—	—	—	—
<u>Vaccinium vitis-idaea</u>	21	29	2	4	—	—	—	—
Herbs:								
<u>Calamagrostis</u> spp.	45	34	1	2	—	—	—	—
<u>Cornus canadensis</u>	55	38	3	4	—	—	—	—
<u>Epilobium angustifolium</u>	50	40	3	4	—	—	—	—
<u>Equisetum arvense</u> <u>8/</u>	51	42	10	13	—	—	—	—
<u>Equisetum scirpoides</u>	0	0	0	0	—	—	—	—
<u>Galium boreale</u>	16	28	1	1	—	—	—	—
<u>Geocaulon lividum</u>	6	12	<u>9/</u>	<u>9/</u>	—	—	—	—
<u>Lycopodium annotinum</u> <u>10/</u>	6	14	<u>9/</u>	<u>1</u>	—	—	—	—
<u>Mertensia paniculata</u>	13	20	<u>9/</u>	<u>1</u>	—	—	—	—
<u>Moehringia lateriflora</u>	20	18	<u>9/</u>	<u>9/</u>	—	—	—	—
<u>Pyrola asarifolia</u> <u>11/</u>	9	11	<u>9/</u>	<u>9/</u>	—	—	—	—
<u>Pyrola secunda</u>	9	14	<u>9/</u>	<u>9/</u>	—	—	—	—

See footnotes at end of table.

Table 19—Quantitative description of the hardwood stage of plant succession on white spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/ (continued)

Species and litter component 2/	Quantitative description of the hardwood stage							
	Frequency 3/		Cover 4/		Density 5/		D.b.h. 6/	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Mosses:								
<i>Ceratodon purpureus</i>	3	6	9/	9/	--	--	--	--
<i>Dicranum</i> spp.	7	0	9/	9/	--	--	--	--
<i>Drepanocladus uncinatus</i>	16	18	9/	9/	--	--	--	--
<i>Hylocomium splendens</i>	21	29	6	18	--	--	--	--
<i>Marchantia polymorpha</i>	0	0	0	0	--	--	--	--
<i>Pleurozium schreberi</i>	24	24	2	4	--	--	--	--
<i>Polytrichum</i> spp.	11	20	1	2	--	--	--	--
Lichens:								
<i>Cladonia</i> spp. 12/	12	19	9/	1	--	--	--	--
<i>Peltigera</i> spp.	4	10	9/	9/	--	--	--	--
Litter component:								
Charred material	1	3	9/	9/	--	--	--	--
Leaves and twigs	99	4	86	5	--	--	--	--
Dead wood and fallen logs	77	24	6	4	--	--	--	--

1/ Number of stands sampled: 11; age: mean 87 years after fire (standard deviation 38); number of species found: mean 24 (standard deviation 5); depth of organic layer: mean 11 cm (standard deviation 3).

2/ Only species with a frequency of at least 30 percent in at least 1 stand are listed in tables 15–20. Not all of those species occur in every stage of succession; all are listed for each stage, however, to enhance comparison of their development.

3/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

4/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

5/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

6/ D.b.h. is the diameter of a tree at breast height. The values given are for trees 2.5 cm in d.b.h. or larger and are based on the equation: D.b.h. = Σ (mean d.b.h. values for a species in a stand) \div total number of stands sampled.

7/ Includes *Alnus tenuifolia* from river-bottom sites.

8/ Includes *Equisetum pratense*.

9/ Less than 0.5 percent.

10/ Includes *Lycopodium clavatum*.

11/ Includes *Pyrola chlorantha*.

12/ Includes *Cladina* spp.

Table 20—Quantitative description of the spruce stage of plant succession on white spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/

Species and litter component <u>2/</u>	Quantitative description of the spruce stage							
	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
----- Percent -----				Stems/ha		Centimeters		
Tree layer:								
<u>Betula papyrifera</u> —								
Mature trees	25	24	—	—	40	39	34.1	0.4
Saplings	20	17	—	—	6	4	1.4	0.3
Seedlings	5	10	—	—	375	750	—	—
<u>Picea glauca</u> —								
Mature trees	100	0	—	—	512	22	19.1	6.1
Saplings	26	46	—	—	10	18	1.1	0.6
Seedlings	29	6	—	—	1,719	493	—	—
<u>Populus balsamifera</u> —								
Mature trees	2	5	—	—	7	14	29.4	3.3
Saplings	9	12	—	—	2	3	0.8	0.2
Seedlings	0	0	—	—	0	0	—	—
<u>Populus tremuloides</u> —								
Mature trees	4	5	—	—	7	10	28.8	2.7
Saplings	1	2	—	—	7/	1	0.8	0
Seedlings	6	10	—	—	562	1,043	—	—
Tall shrubs:								
<u>Alnus crispa</u> <u>8/</u>	12	10	—	—	2,594	4,137	—	—
<u>Rosa acicularis</u>	76	18	—	—	14,125	4,071	—	—
<u>Rubus idaeus</u>	0	0	—	—	0	0	—	—
<u>Salix arbusculoides</u>	0	0	—	—	0	0	—	—
<u>Salix bebbiana</u>	0	0	—	—	0	0	—	—
<u>Salix glauca</u>	0	0	—	—	0	0	—	—
Other <u>Salix</u> spp.	0	0	—	—	0	0	—	—
<u>Viburnum edule</u>	39	15	—	—	5,062	5,508	—	—
Low shrubs:								
<u>Ledum groenlandicum</u>	0	0	0	0	—	—	—	—
<u>Linnaea borealis</u>	52	45	6	5	—	—	—	—
<u>Vaccinium vitis-idaea</u>	11	22	1	2	—	—	—	—
Herbs:								
<u>Calamagrostis</u> spp.	20	19	1	7/	—	—	—	—
<u>Cornus canadensis</u>	15	20	1	1	—	—	—	—
<u>Epilobium angustifolium</u>	14	21	7/	7/	—	—	—	—
<u>Equisetum arvense</u> <u>9/</u>	84	5	4	2	—	—	—	—
<u>Equisetum scirpoides</u>	0	0	0	0	—	—	—	—
<u>Galium boreale</u>	20	24	7/	7/	—	—	—	—
<u>Geocaulon lividum</u>	60	13	3	2	—	—	—	—
<u>Lycopodium annotinum</u> <u>10/</u>	0	0	0	0	—	—	—	—
<u>Mertensia paniculata</u>	19	16	7/	7/	—	—	—	—
<u>Moehringia lateriflora</u>	11	13	7/	7/	—	—	—	—
<u>Pyrola asarifolia</u> <u>11/</u>	32	26	1	7/	—	—	—	—
<u>Pyrola secunda</u>	26	27	1	1	—	—	—	—

See footnotes at end of table.

Table 20—Quantitative description of the spruce stage of plant succession on white spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/ (continued)

Species and litter component <u>2/</u>	Quantitative description of the spruce stage							
	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Mosses:								
<u>Ceratodon purpureus</u>	2	3	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Dicranum spp.</u>	8	9	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Drepanocladus uncinatus</u>	4	2	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Hylocomium splendens</u>	91	6	61	10	—	—	—	—
<u>Marchantia polymorpha</u>	0	0	0	0	—	—	—	—
<u>Pleurozium schreberi</u>	34	18	5	4	—	—	—	—
<u>Polytrichum spp.</u>	2	5	<u>7/</u>	<u>7/</u>	—	—	—	—
Lichens:								
<u>Cladonia spp. <u>12/</u></u>	24	19	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Peltigera spp.</u>	21	10	<u>1</u>	<u>1</u>	—	—	—	—
Litter component:								
Charred material	0	0	0	0	—	—	—	—
Leaves and twigs	98	5	26	11	—	—	—	—
Dead wood and fallen logs	78	23	16	4	—	—	—	—

1/ Number of stands sampled: 4; age: mean 170 years after fire (standard deviation 70); number of species found: mean 30 (standard deviation 1); depth of organic layer: mean 12 cm (standard deviation 1).

2/ Only species with a frequency of at least 30 percent in at least 1 stand are listed in tables 15–20. Not all of those species occur in every stage of succession; all are listed for each stage, however, to enhance comparison of their development.

3/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

4/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

5/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

6/ D.b.h. is the diameter of a tree at breast height. The values given are for trees 2.5 cm in d.b.h. or larger and are based on the equation: D.b.h. = Σ (mean d.b.h. values for a species in a stand) \div total number of stands sampled.

7/ Less than 0.5 percent.

8/ Includes Alnus tenuifolia from river-bottom sites.

9/ Includes Equisetum pratense.

10/ Includes Lycopodium clavatum.

11/ Includes Pyrola chlorantha.

12/ Includes Cladonia spp.

Table 21—Summary of the quantitative descriptions of the 6 stages of plant succession on white spruce sites in the taiga of Interior Alaska 1/

Item	Newly burned stage		Moss-herb stage		Tall shrub-sapling stage		Dense tree stage		Hardwood stage		Spruce stage	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
Stand age, years	0.5	0.6	4	2	15	8	36	7	87	38	170	70
Plant species found, number 2/	12	3	20	6	30	11	29	4	24	5	30	1
Depth of organic layer, centimeters	NA	NA	3	1	8	6	8	3	11	3	12	1
Number of stems per hectare												
Density: 3/ 4/												
Tree layer—												
Mature trees	5/ (966)	(730)	(202)	(372)	124	193	2,319	1,598	909	405	566	26
Saplings	2	4	2,417	4,191	3,256	6,966	52	70	55	144	18	21
Seedlings	30,000	46,558	63,203	70,929	31,792	32,908	1,650	2,536	22,488	68,100	2,656	2,095
Tall shrub layer—												
Salix spp.	5,250	5,990	2,547	1,939	21,737	29,203	825	1,310	648	1,136	0	0
Other tall shrubs	83,688	57,134	17,344	36,848	75,889	122,141	16,075	11,228	58,170	70,976	21,781	6,708
Percent												
Cover: 4/ 6/												
Low shrubs	7/	7/	7	7	6	10	14	15	7	8	7	6
Herbs	13	10	30	25	45	33	10	6	21	15	10	4
Mosses	0	0	22	19	8	10	14	10	11	24	69	12
Lichens	0	0	2	3	4	8	2	2	1	1	2	1
Litter components	118	9	83	26	90	18	93	7	92	25	42	13

NA = not available.

1/ Number of stands sampled: newly burned, 4; moss-herb, 8; tall shrub-sapling, 9; dense tree, 5; hardwood, 11; spruce, 4.

2/ Also includes the 3 stages of tree development: mature tree, sapling, and seedling. When present, each stage of a species is counted as 1.

3/ The computed or counted number of stems occurring in a given area.

4/ Totals may be off because of rounding and because data listed were only for the species occurring most frequently.

5/ Numbers in parentheses indicate the number of trees that originated before the fire.

6/ The percent of area shaded by the canopy of a given plant layer or litter component.

7/ Less than 0.5 percent.

Patterns of Change on White Spruce Sites

Although each developmental stage can be described individually, together they form patterns that change through time. Figure 19 illustrates the changes; each graph in the figure is limited to one stratum.

Trees start in great numbers as seedlings and suckers. Most of them will die, but some do become saplings and then trees (fig. 19A). Seedlings (and saplings) are most numerous in the moss-herb stage, are least numerous in the dense tree and spruce stages, but are always present (fig. 19B). Quaking aspen and paper birch dominate throughout. Saplings peak in the tall shrub-sapling stage; beginning with the dense tree stage, they are present only in minimal amounts (fig. 19C). Trees peak in the dense tree stage and decline thereafter (fig. 19D). Hardwoods dominate the dense tree and hardwood stages, and spruce dominates the spruce stage.

Willows first appear as sucker shoots and seedlings in the newly burned stage, hold their own in the moss-herb stage, and attain their maximum growth and numbers in the tall shrub-sapling stage (fig. 19E). After that, they decline rapidly and completely disappear sometime in the hardwood stage. Littletree and Bebb are the last to die out. Bebb and grayleaf appear, from the study data, to be the most common of the willow species.

The non-willow tall shrubs show a more complex pattern (fig. 19F). American green alder appears by the end of the moss-herb stage and increases continuously, reaching its greatest density, only 2,600 stems/ha, in the spruce stage. Prickly rose and high bushcranberry are always present. Sometimes one is more dense, sometimes the other. Numbers of both are high in the newly burned, tall shrub-sapling, and hardwood stages; however, each successive peak is slightly lower. This may be caused by stand differences or it may be successful establishment and then opportunism. More study is required to distinguish which is the case.

Low shrubs appear early, are always present, and reach a peak in area covered during the hardwood stage (fig. 19G). Within this pattern, however, two trends are apparent: (1) Twin-flower is established by the end of the moss-herb stage and increases thereafter to become the primary low shrub species in the spruce stage; and (2) mountain-cranberry and Labrador-tea peak primarily in the dense tree stage and decline thereafter. Other species occur too sporadically to show trends.

The herb layer begins to develop immediately after fire, increases steadily in total cover, peaks early in the tall shrub stage, and declines thereafter but never disappears (fig. 19H). Not all herb species, however, follow this pattern. Some, such as Geocaulon lividum, occur in small amounts through the dense tree stage and increase in the spruce stage. Others, such as fireweed, appear early, reach their peak in the moss-herb stage, and decrease thereafter. Still others, including most herb species, are always present in varying amounts but develop their greatest cover early in the tall shrub-sapling stage. Of these, field horsetail, reedgrass, and bunchberry account for most of the coverage.

Mosses peak twice, first a small peak in the moss-herb stage and then a larger peak in the spruce stage (fig. 19I). Within this trend three patterns are apparent. (1) Feathermosses, especially Hylocomium splendens, appear by the end of the tall shrub stage, start expanding in the dense tree stage, and blanket the ground in the spruce stage. Of the feathermosses, Pleurozium schreberi is most extensive in the dense tree stage. In the later hardwood stage, Hylocomium splendens is more extensive. (2) Ceratodon purpureus and Marchantia polymorpha cover extensive areas early in succession, peak in the moss-herb stage, and essentially disappear by the beginning of the dense tree stage. (3) Still others, such as Polytrichum spp., tend to be more extensive in the younger stages but are always present and may be locally abundant at any time.

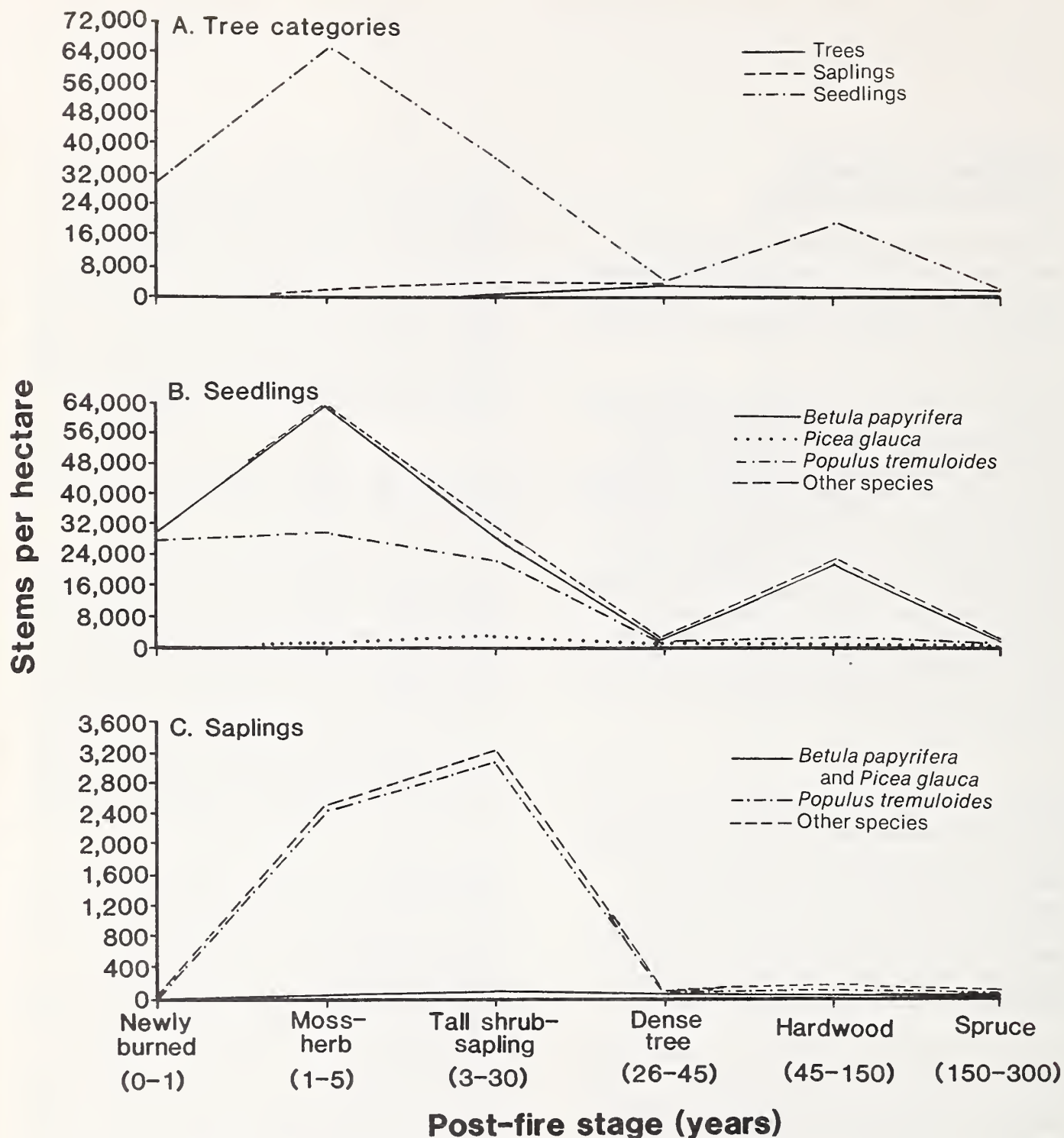


Figure 19.—Successional trends on white spruce sites. Shown are densities of A, tree categories; B, seedlings; C, saplings; D, trees; E, tall shrubs, willow; and F, tall shrubs, non-willow. Also shown are the covers of G, low shrubs; H, herbs; I, mosses and

liverworts; J, lichens; and K, litter. Other items shown are L, depth of organic layer; and M, number of species present. Each line represents the number occurring of that unit. Graphs with more than one line show cumulative totals.

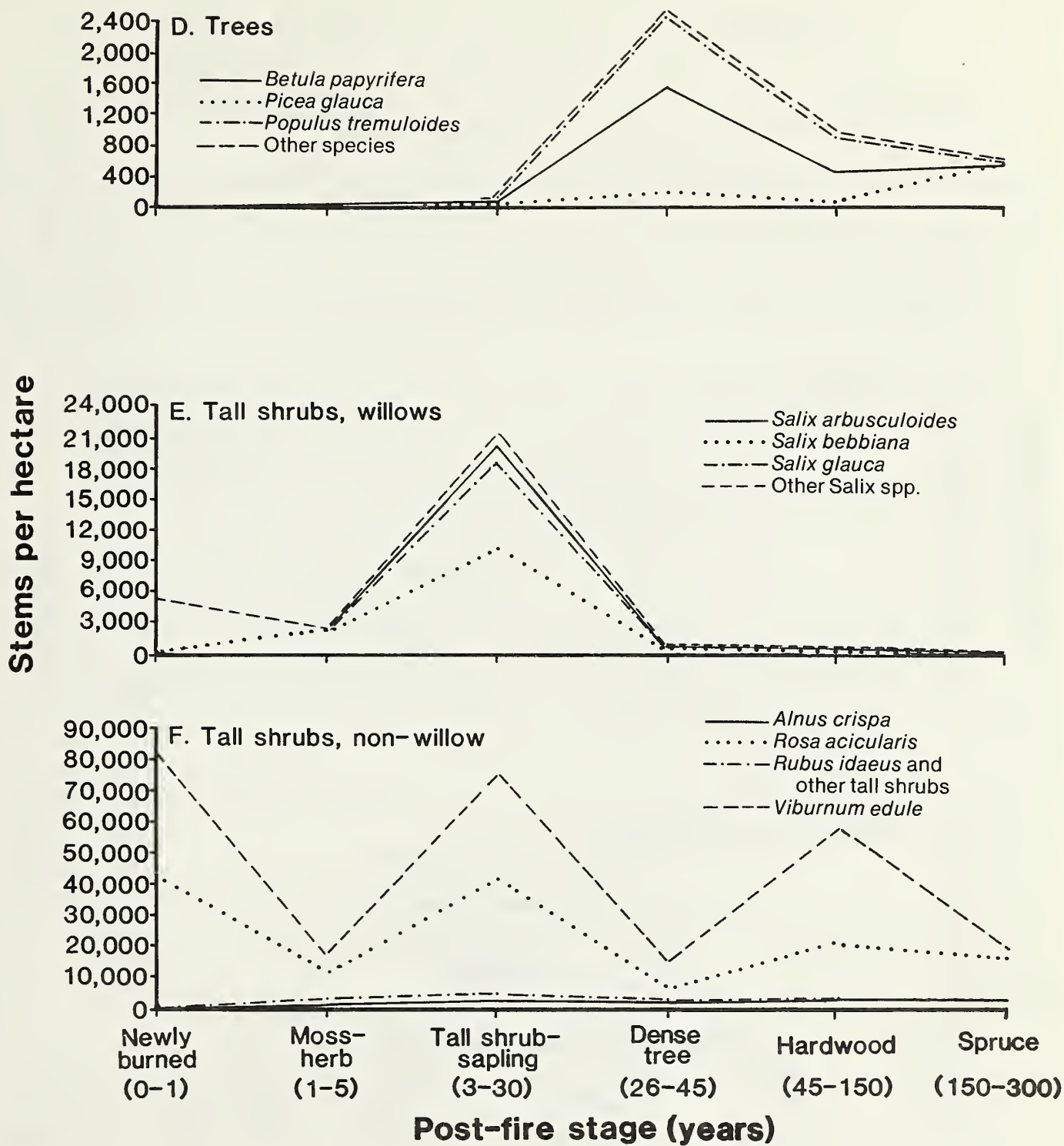


Figure 19.—(continued)

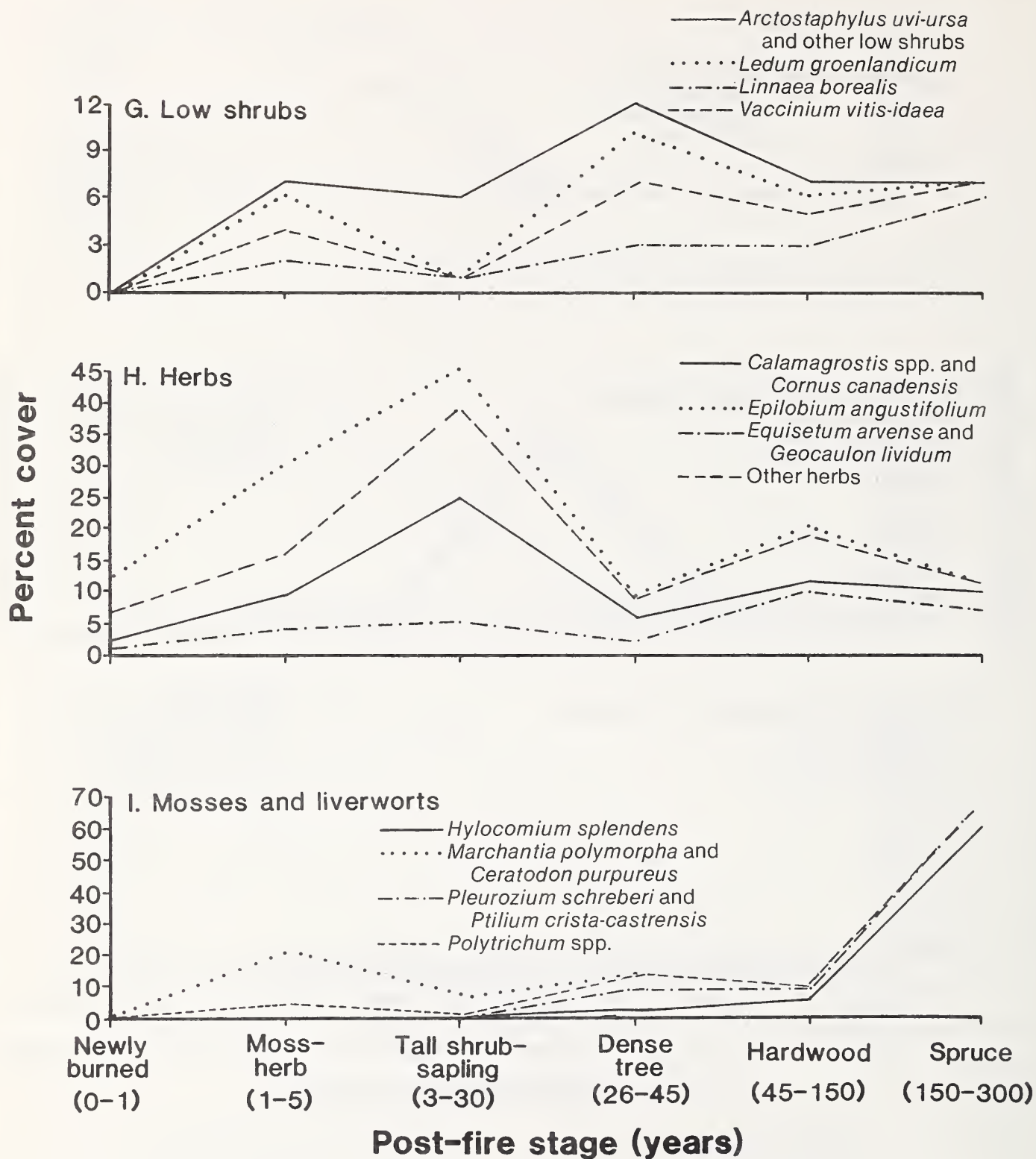


Figure 19.—(continued)

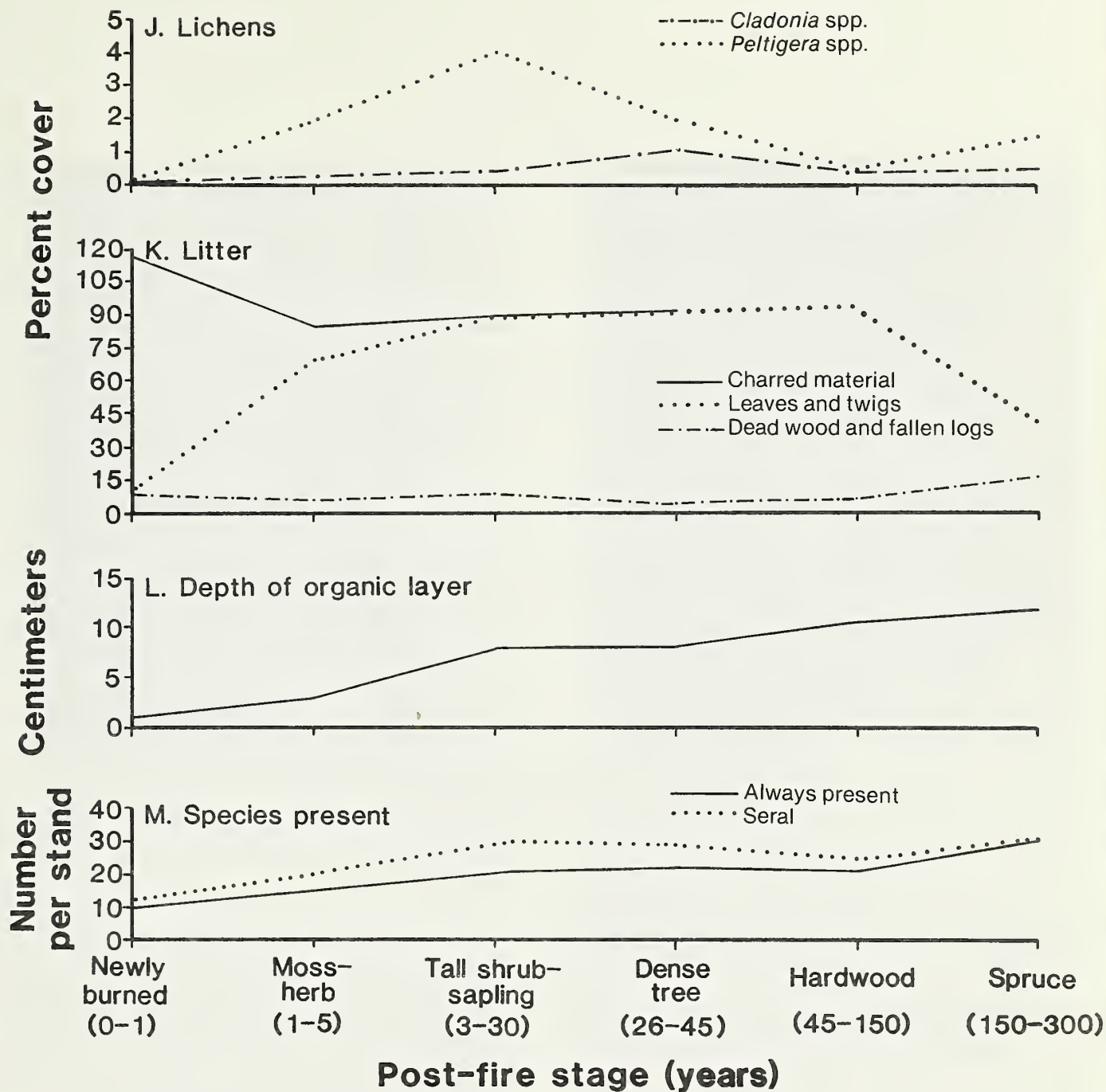


Figure 19.—(continued)

Ground lichens are always present in small quantities (fig. 19J). Peltigera spp. appear to peak in the tall shrub stage, and Cladonia spp. peak in the dense tree stage.

Decaying logs occur on the forest floor in small numbers at all times, but the numbers increase with the passing of the hardwood stage (fig. 19K). Leaf and twig litter increases as the deciduous vegetation develops, peaks in the tall shrub, dense tree, and hardwood stages, and then declines in the spruce stage. Charred ground surfaces, which are extensive after fire, disappear rapidly and are gone by the end of the moss-herb stage.

The organic layer reflects the accumulation of litter (fig. 19L). New litter keeps falling; old litter decomposes and becomes more dense. As this happens, the organic layer gradually thickens from almost nothing after fire to 12 cm in old stands.

Lastly, the number of species present in a given area increases continuously well into the tall shrub-sapling stage and then remains almost constant (fig. 19M). Most species are present throughout succession but in varying amounts. Other species occur in some stages but not all. Ceratodon purpureus, Marchantia polymorpha, fireweed, willows, hardwoods, and Cladonia spp. are examples of the latter group.

The end of succession is a fairly open to closed stand of large white spruce under which prickly rose, high bushcranberry, twin-flower, and a continuous blanket of Hylocomium splendens are usually found (see figs. 6 and 7).

The six mature forest community types that occur on white spruce sites and are described in this paper can now be seen in perspective. Each is mature in the sense that the dominating trees are at their best development; however, in theory at least, the spruce-dominated types are farthest along in terms of succession. Evidence suggests that, in the absence of fire, other stands will become white spruce types in time.

Stages on Mesic Black Spruce Sites

1.—The newly burned stage (0–1 year after fire) is a time of initial impact and recovery (fig. 20). Fire is usually a combination of ground and crown fires that leave the vegetation in a mosaic of conditions. Small patches of exposed mineral soil are common and usually intermixed with larger patches of partially burned or unburned vegetation on the forest floor. Trees are usually killed except in "stringers," areas left completely untouched by fire. Within days, shoots appear. Willow, prickly rose, bog blueberry, Labrador-tea, cloudberry, reedgrass, and Polytrichum spp. can be among the first. Soon willow seedlings, moss protonema, and liverwort thalli also become visible.

Tables 22 and 28 (p. 80 and 92), give the findings from the stands studied. Bog blueberry, Labrador-tea, reedgrass, and cloudberry were found in all newly burned stands; and willow, prickly rose, woodland horsetail, and Polytrichum spp. occurred in most stands. The depth of the organic layer was quite variable but averaged 11 cm. Depth to permafrost varied but averaged 49 cm.

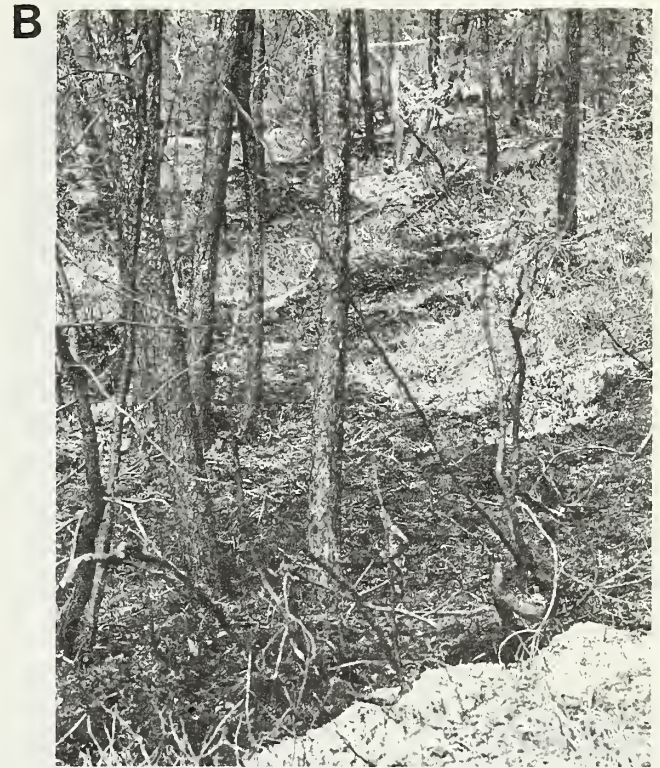
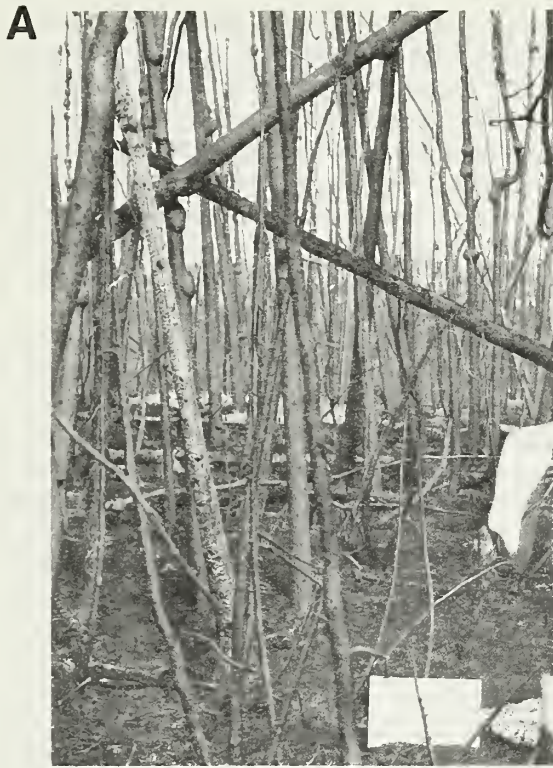


Figure 20.—Newly burned stage on black spruce sites 2 months after fire: A, Severely burned area (stand no. 002); B, lightly burned patches among moderately burned areas (stand no. 006).

At the end of the first growing season after fire, willows (mostly Scouler) averaged 1,181 stems/ha; other tall shrubs (mostly prickly rose) averaged 625 stems/ha. Low shrubs (bog blueberry and Labrador-tea) covered, on the average, 1 percent of the area, herbs (mostly

reedgrass and cloudberry) covered an additional 1 percent, while mosses and lichens together covered less than 1 percent of the ground. Charred material was visible on 96 percent of the forest floor. Revegetation had begun but areas still looked mostly black.

A



Figure 21.—Moss-herb stage on black spruce sites: A, Low shrubs and bare patches dominate the forest floor in this 4-year-old stand (no. 109) which had been lightly to moderately burned; B, a 3-year-old black spruce stand (BS-3H) which had been severely burned.

B



2.—The moss-herb stage (1–5 years after fire) is a time of introduction and expansion of species (fig. 21). The number of species present will double during this stage. In addition to the species found at the end of the newly burned stage, black spruce, quaking aspen, paper birch, numerous willow species, resin birch, mountain-cranberry, Ceratodon purpureus, and Marchantia polymorpha were common. Ceratodon purpureus, Marchantia polymorpha, and all tree seedlings do best on areas of moist mineral soil. Shoots appear on both mineral soil and organic surfaces, provided vegetative parts exist underground. In 2-year-old stands, the organic layer averaged 15 cm in depth, and charred surfaces remained visible on 76 percent of the forest floor. The unshaded and blackened ground is an excellent heat sink. Consequently, both the active thaw zone and the depth to permafrost increase.

Densities averaged 17,954 stems/ha for black spruce; 10,901 for quaking aspen (sucker shoots and seedlings), and 355 seedlings/ha for paper birch (tables 23 and 28, p. 82 and 92). Willows (one-half diamondleaf and one-fourth Scouler) averaged 1,392 stems/ha, whereas other tall shrubs (mostly prickly rose and resin birch) averaged 3,362. Low shrubs (mostly bog blueberry, Labrador-tea, and mountain-cranberry) covered, on the average, 10 percent of the area, and herbs (mostly reedgrass, cloudberry, and woodland horsetail) covered 11 percent. Mosses (mostly Ceratodon purpureus, Sphagnum spp., and Polytrichum spp.) covered 14 percent of the area.

With time, many plants will spread into surrounding areas and the taller growing species will overtop the remaining vegetation; the tall shrub-sapling stage will develop.

3.—During the tall shrub-sapling stage (5–30 years after fire), the vegetation is dominated by tall shrubs and/or saplings in the overstory with mosses, herbs, low shrubs, and tree seedlings below (fig. 22). The vegetation is basically a continuation of that established earlier, but additional species become established. Lichens are sometimes present but only in small amounts.

Ten years after fire, willows, the most visually dominant vegetation in the stands studied, averaged 14,859 stems/ha and stood 1–5 m tall (tables 24 and 28, p. 84 and 92). Half the willows were Bebb, the other half mostly Scouler, diamondleaf, grayleaf, littletree, and feltleaf. Other tall shrubs (one-third prickly rose and one-third resin birch) averaged 5,977 stems/ha. Saplings (mostly quaking aspen) averaged 1,461 stems/ha; seedlings (over one-half black spruce and one-third hardwoods) averaged 22,589. The lower growing vegetation was dominated by mosses (mostly Ceratodon purpureus), herbs (mostly reedgrass and fireweed), and low shrubs (bog blueberry, Labrador-tea, and mountain-cranberry). Total cover averaged 37, 18, and 15 percent for mosses, herbs, and low shrubs, respectively. Charred surfaces were still visible on 20 percent of the area and deadfall litter covered about half the ground. The organic layer averaged 17 cm in depth, and the active thaw zone extended to a depth of 82 cm.

As this stage advances, herbs become less extensive, low shrubs and mosses cover increasingly more area, while saplings grow into trees.

4.—The dense tree stage (30–55 years after fire) is characterized by numerous young trees in the overstory and extensive patches of low shrubs, feathermosses, and lichens below (fig. 23). Other mosses, Polytrichum spp. and Dicranum spp., occur in small amounts. Tall shrubs and herbs are sometimes present. Litter occurs but is rapidly incorporated in the moss layer.



Figure 22.—Tall shrub-sapling stage on black spruce sites. This is a 23-year-old spruce-hardwood stand (no. 146).



Figure 23.—Dense tree stage on black spruce sites. This 70-year-old black spruce/feathermoss-lichen stand (no. 132) has 2,080 trees/ha.

Trees (mostly black spruce) in 50-year-old stands sampled averaged 2,595 stems/ha, 5.4-cm d.b.h., and 5-7 m tall (tables 25 and 28, p. 86 and 92). Saplings (mostly black spruce) averaged 1,682 stems/ha. Low shrubs (one-half mountain-cranberry, one-fourth bog blueberry, and one-fourth Labrador-tea) covered, on the average, 32 percent of the ground. Mosses covered 60 percent of the forest floor. Of the mosses, Pleurozium schreberi dominated with an average cover of 36 percent; Hylocomium splendens, Sphagnum spp., Polytrichum spp., and Dicranum spp. occurred in lesser amounts. Lichens (one-fourth Peltigera spp., one-fourth Cladonia spp., and one-fourth Cladonia spp.) covered 18 percent of the area. Willows, mostly Scouler, were infrequent averaging 1,261 stems/ha. Other tall shrubs (resin birch, prickly rose, and American green alder) averaged 5,396. Herbs (mostly reedgrass, cloudberry, and Geocaulon lividum), covered 5 percent of the ground. Litter was visible on 23 percent of the forest floor and logs on 6 percent. Charred ground was no longer exposed. The depth of the organic layer averaged 17 cm, and the permafrost table lay 82 cm below the surface.

As stands of the dense tree stage develop, trees self-thin, the survivors increase in height and diameter, and the feathermoss and low shrub layers continue to expand.

Snags, dead lower branches, and a well-developed layer of low shrubs, feathermosses, and lichens make these stands flammable. Fire terminates succession in many stands during this stage. Other stands evolve into either the hardwood-spruce stage or the spruce stage, depending on the presence or absence of quaking aspen or paper birch.

5.—The mixed hardwood-spruce stage (56-90 years after fire) is characterized by a mixed canopy of black spruce, quaking aspen, and/or paper birch (see figs. 9 and 10). The hardwoods sometimes dominate but more often do not. In either case, this is the period in which the hardwood trees are mature. As the stage progresses, the hardwoods will stagnate and die. On the forest floor, prickly rose, low shrubs, a few herbs, and feathermosses are usually found. In general, when few hardwoods are present, feathermosses cover extensive areas of the forest floor. But when hardwoods are numerous, leaf litter, not feathermoss, dominates the forest floor.

The stands studied averaged 70 years in age. Trees averaged 2,211 stems/ha and were one-fourth hardwoods and three-fourths black spruce (tables 26 and 28, p. 88 and 92). . Quaking aspen averaged 15.6-cm d.b.h., paper birch 11.9-cm d.b.h., and black spruce 7.3-cm d.b.h. All trees were 5-15 m tall. Willows (mostly Bebb) averaged 1,136 stems/ha, other tall shrubs (two-thirds prickly rose and one-third American green alder) averaged 3,920, and tree seedlings (mostly black spruce) averaged 10,125. Low shrubs (mostly mountain-cranberry and bog blueberry) covered, on the average, 17 percent of the area, herbs (mostly reedgrass and bunchberry) covered 6 percent, and mosses (half Pleurozium schreberi and half Hylocomium splendens) covered 7 percent. Litter covered 46 percent of the forest floor and logs were found on 5 percent of the ground surface. The organic layer averaged 14 cm in thickness and depth to permafrost was 57 cm.

As this stage ages, the hardwoods stagnate and die, producing increasingly pure stands of spruce. Like stands in the dense tree stage, spruce-hardwood stands are quite flammable because of both live and dead material on the forest floor. Each year, fire burns many stands in this development stage. In the absence of fire, however, the spruce stage will evolve.

6.--The spruce stage (91-200+ years after fire) is the oldest of the mesic black spruce stages. The overstory is mostly black spruce, although in a few locations white spruce and relic paper birch may occur (see figs. 11 and 12). American green alder, smaller black spruce, and sometimes prickly rose form a mid-height layer beneath the trees. The forest floor is dominated by feathermosses, Sphagnum spp., low shrubs, litter, and herbs. Permafrost is frequently present. As the stand ages, the mounds of Sphagnum spp. become larger, the moss layer thicker, and the permafrost table closer to the soil surface.

This stage is seldom found in the forest landscape since most stands succumb to fire before they develop to this point; however, they do exist. Those surveyed in this study averaged 121 years in age. Black spruce trees averaged 1,800 stems/ha, 15.2-cm d.b.h., and 11 m in height (tables 27 and 28, p. 90 and 92). Saplings and seedlings (again mostly black spruce) averaged 225 and 4,719 stems/ha, respectively. Many so-called seedlings are really layerings or lower tree branches that rooted and turned skyward after they were

buried by the thickening moss layer. Tall shrubs (two-thirds American green alder and one-third prickly rose) averaged 7,750 stems/ha. Low shrubs (one-half mountain-cranberry and one-fourth Labrador-tea) covered, on the average, 29 percent of the forest floor, while herbs (mostly reedgrass and Geocaulon lividum) covered 16 percent. Mosses (mostly Pleurozium schreberi and Hylocomium splendens) covered 80 percent and lichens (mostly Cladina rangiferina and Cetraria cucullata) covered 2 percent of the forest floor. Litter was visible on 18 percent of the forest floor, and logs on an additional 6 percent. The organic layer averaged 16 cm in depth. Permafrost was found 59 cm beneath the ground surface.

These stands will live until burned or impacted by other disturbances. As they age, the moss layer continues to thicken, the soil temperature slowly drops, the permafrost table moves closer to the surface, and growth stagnates. The oldest stands in this study were around 200 years old.

Tables 22-27 are grouped together on p. 80-91 to aid the reader in following the succession of common species on mesic black spruce sites through the six developmental stages. A summary appears in table 28, p. 92.

Table 22—Quantitative description of the newly burned stage of plant succession on mesic black spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/

Quantitative description of the newly burned stage								
Species and litter component 2/	Frequency 3/		Cover 4/		Density 5/		D.b.h. 6/	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
----- Percent -----			Stems/ha			Centimeters		
Tree layer:								
<u>Betula papyrifera</u> —								
Mature trees	0	0	—	—	0	0	—	—
Saplings	0	0	—	—	0	0	—	—
Seedlings	0	0	—	—	0	0	—	—
<u>Picea glauca</u> —								
Mature trees	0	0	—	—	0	0	—	—
Saplings	0	0	—	—	0	0	—	—
Seedlings	0	0	—	—	0	0	—	—
<u>Picea mariana</u> —								
Mature trees	0	0	—	—	0	0	—	—
Saplings	0	0	—	—	0	0	—	—
Seedlings	0	0	—	—	0	0	—	—
<u>Populus tremuloides</u> —								
Mature trees	0	0	—	—	0	0	—	—
Saplings	0	0	—	—	0	0	—	—
Seedlings	0	0	—	—	0	0	—	—
Tall shrub layer:								
<u>Alnus crispa</u>	3	6	—	—	83	144	—	—
<u>Alnus tenuifolia</u>	0	0	—	—	0	0	—	—
<u>Betula glandulosa</u>	2	3	—	—	42	72	—	—
<u>Rosa acicularis</u>	18	24	—	—	500	661	—	—
<u>Rubus idaeus</u>	0	0	—	—	0	0	—	—
<u>Salix alaxensis</u>	0	0	—	—	0	0	—	—
<u>Salix arbusculoides</u>	0	0	—	—	0	0	—	—
<u>Salix bebbiana</u>	0	0	—	—	0	0	—	—
<u>Salix glauca</u>	0	0	—	—	0	0	—	—
<u>Salix planifolia</u>								
ssp. <u>pulchra</u>	3	3	—	—	250	331	—	—
<u>Salix scouleriana</u>	5	9	—	—	792	1,371	—	—
Other <u>Salix</u> spp.	0	0	—	—	0	0	—	—
Low shrub layer:								
<u>Empetrum nigrum</u>	0	0	0	0	—	—	—	—
<u>Ledum decumbens</u>	0	0	0	0	—	—	—	—
<u>Ledum groenlandicum</u>	37	25	7/	7/	—	—	—	—
<u>Vaccinium oxycoccus</u>	0	0	0	0	—	—	—	—
<u>Vaccinium uliginosum</u>	38	28	7/	7/	—	—	—	—
<u>Vaccinium vitis-idaea</u>	5	5	7/	7/	—	—	—	—
Herb layer:								
<u>Calamagrostis</u> spp.	71	6	1	7/	—	—	—	—
<u>Cornus canadensis</u>	3	6	7/	7/	—	—	—	—
<u>Epilobium angustifolium</u>	0	0	0	0	—	—	—	—
<u>Equisetum arvense</u>	0	0	0	0	—	—	—	—
<u>Equisetum scirpoides</u>	0	0	0	0	—	—	—	—
<u>Equisetum sylvaticum</u>	10	10	7/	7/	—	—	—	—
<u>Geocaulon lividum</u>	2	3	7/	7/	—	—	—	—
<u>Lycopodium annotinum</u> 8/	0	0	0	0	—	—	—	—
<u>Mertensia paniculata</u>	0	0	0	0	—	—	—	—
<u>Petasites frigidus</u>	3	6	7/	7/	—	—	—	—
<u>Rubus chamaemorus</u>	32	14	1	7/	—	—	—	—

See footnotes at end of table.

Table 22—Quantitative description of the newly burned stage of plant succession on mesic black spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/ (continued)

Species and litter component <u>2/</u>	Quantitative description of the newly burned stage							
	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- <u>Percent</u> -----				<u>Stems/ha</u>		<u>Centimeters</u>	
Mosses:								
<u>Aulacomnium palustre</u>	0	0	0	0	—	—	—	—
<u>Aulacomnium turgidum</u>	0	0	0	0	—	—	—	—
<u>Ceratodon purpureus</u>	0	0	0	0	—	—	—	—
<u>Dicranum spp.</u>	0	0	0	0	—	—	—	—
<u>Drepanocladus uncinatus</u>	0	0	0	0	—	—	—	—
<u>Hylocomium splendens</u>	0	0	0	0	—	—	—	—
<u>Marchantia polymorpha</u>	0	0	0	0	—	—	—	—
<u>Pleurozium schreberi</u>	0	0	0	0	—	—	—	—
<u>Polytrichum spp.</u>	13	19	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Sphagnum spp.</u>	0	0	0	0	—	—	—	—
Unidentified moss	3	6	<u>7/</u>	<u>7/</u>	—	—	—	—
Lichens:								
<u>Cetraria cucullata</u>	0	0	0	0	—	—	—	—
<u>Cetraria islandica</u>	0	0	0	0	—	—	—	—
<u>Cladina arbuscula</u>	0	0	0	0	—	—	—	—
<u>Cladina rangiferina</u>	2	3	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Cladonia spp. 9/</u>	0	0	0	0	—	—	—	—
<u>Nephroma arcticum</u>	0	0	0	0	—	—	—	—
<u>Peltigera aphthosa</u>	0	0	0	0	—	—	—	—
<u>Peltigera spp. 10/</u>	2	3	<u>7/</u>	<u>7/</u>	—	—	—	—
Litter components:								
Charred material	100	0	96	2	—	—	—	—
Leaves and twigs	98	3	8	1	—	—	—	—
Dead wood and fallen logs	100	0	2	1	—	—	—	—

1/ Number of stands sampled: 3; age: mean 5 weeks after fire (standard deviation 0); number of species found: mean 12 (standard deviation 3); depth of organic layer: mean 11 cm (standard deviation 8); depth of active thaw zone: mean 49 cm (standard deviation 9).

2/ Only species with a frequency of at least 30 percent in at least 1 stand are listed in tables 22-27. Not all of those species occur in every stage of succession; all are listed for each stage, however, to enhance comparison of their development.

3/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

4/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

5/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

6/ D.b.h. is the diameter of a tree at breast height. The values given are for trees 2.5 cm in d.b.h. or larger and are based on the equation: D.b.h. = Σ (mean d.b.h. values for a species in a stand) \div total number of stands sampled.

7/ Less than 0.5 percent.

8/ Includes Lycopodium clavatum.

9/ Includes Cladonia amaurocraea, C. alpestris, and Cladina spp.

10/ Includes Peltigera canina.

Table 23—Quantitative description of the moss-herb stage of plant succession on mesic black spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/

Quantitative description of the moss-herb stage								
Species and litter component 2/	Frequency 3/		Cover 4/		Density 5/		D.b.h. 6/	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
----- Percent -----								
Stems/ha								
Centimeters								
Tree layer:								
<u>Betula papyrifera—</u>								
Mature trees	0	0	—	—	0	0	—	—
Saplings	0	0	—	—	0	0	—	—
Seedlings	2	4	—	—	355	1,263	—	—
<u>Picea glauca—</u>								
Mature trees	0	0	—	—	0	0	—	—
Saplings	0	0	—	—	0	0	—	—
Seedlings	0	0	—	—	0	0	—	—
<u>Picea mariana—</u>								
Mature trees	7/ (23)	(39)	—	—	(48)	(154)	(6.8)	(1.4)
Saplings	(23)	(40)	—	—	(13)	(23)	(0.6)	(0.9)
Seedlings	58	35	—	—	17,954	14,972	—	—
<u>Populus tremuloides—</u>								
Mature trees	0	0	—	—	0	0	—	—
Saplings	0	0	—	—	0	0	—	—
Seedlings	6	23	—	—	10,901	45,443	—	—
Tall shrub layer:								
<u>Alnus crispa</u>	4	8	—	—	434	1,168	—	—
<u>Alnus tenuifolia</u>	0	0	—	—	0	0	—	—
<u>Betula glandulosa</u>	27	27	—	—	993	1,204	—	—
<u>Rosa acicularis</u>	14	23	—	—	1,928	6,227	—	—
<u>Rubus idaeus</u>	8/	1	—	—	7	29	—	—
<u>Salix alaxensis</u>	0	0	—	—	0	0	—	—
<u>Salix arbusculoides</u>	0	0	—	—	0	0	—	—
<u>Salix bebbiana</u>	3	12	—	—	118	516	—	—
<u>Salix glauca</u>	8/	1	—	—	59	258	—	—
<u>Salix planifolia</u>								
ssp. <u>pulchra</u>	10	12	—	—	728	869	—	—
<u>Salix scouleriana</u>	2	7	—	—	454	1,979	—	—
Other <u>Salix</u> spp.	1	4	—	—	33	101	—	—
Low shrub layer:								
<u>Empetrum nigrum</u>	4	8	8/	8/	—	—	—	—
<u>Ledum decumbens</u>	16	22	8/	1	—	—	—	—
<u>Ledum groenlandicum</u>	65	30	3	3	—	—	—	—
<u>Vaccinium oxycoccus</u>	17	20	1	1	—	—	—	—
<u>Vaccinium uliginosum</u>	62	32	3	3	—	—	—	—
<u>Vaccinium vitis-idaea</u>	53	35	2	3	—	—	—	—
Herb layer:								
<u>Calamagrostis</u> spp.	63	24	3	6	—	—	—	—
<u>Cornus canadensis</u>	7	12	8/	8/	—	—	—	—
<u>Epilobium angustifolium</u>	8	8	8/	8/	—	—	—	—
<u>Equisetum arvense</u>	3	10	8/	8/	—	—	—	—
<u>Equisetum scirpoides</u>	4	16	8/	8/	—	—	—	—
<u>Equisetum sylvaticum</u>	65	40	4	4	—	—	—	—
<u>Geocaulon lividum</u>	2	5	8/	8/	—	—	—	—
<u>Lycopodium annotinum</u> 9/	8/	1	8/	8/	—	—	—	—
<u>Mertensia paniculata</u>	1	4	8/	8/	—	—	—	—
<u>Petasites frigidus</u>	9	10	8/	8/	—	—	—	—
<u>Rubus chamaemorus</u>	54	35	2	2	—	—	—	—

See footnotes at end of table.

Table 23—Quantitative description of the moss-herb stage of plant succession on mesic black spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/ (continued)

Quantitative description of the moss-herb stage								
Species and litter component <u>2/</u>	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Mosses:								
<u>Aulacomnium palustre</u>	10	14	1	1	—	—	—	—
<u>Aulacomnium turgidum</u>	0	0	0	0	—	—	—	—
<u>Ceratodon purpureus</u>	37	39	6	10	—	—	—	—
<u>Dicranum spp.</u>	2	5	<u>8/</u>	<u>8/</u>	—	—	—	—
<u>Drepanocladus uncinatus</u>	0	0	0	0	—	—	—	—
<u>Hylocomium splendens</u>	2	3	<u>8/</u>	1	—	—	—	—
<u>Marchantia polymorpha</u>	6	6	<u>8/</u>	<u>8/</u>	—	—	—	—
<u>Pleurozium schreberi</u>	13	18	1	2	—	—	—	—
<u>Polytrichum spp.</u>	71	27	2	2	—	—	—	—
<u>Sphagnum spp.</u>	19	22	4	5	—	—	—	—
Unidentified moss	9	14	<u>8/</u>	<u>8/</u>	—	—	—	—
Lichens:								
<u>Cetraria cucullata</u>	1	5	<u>8/</u>	<u>8/</u>	—	—	—	—
<u>Cetraria islandica</u>	1	2	<u>8/</u>	<u>8/</u>	—	—	—	—
<u>Cladina arbuscula</u>	1	2	<u>8/</u>	<u>8/</u>	—	—	—	—
<u>Cladina rangiferina</u>	2	5	<u>8/</u>	<u>8/</u>	—	—	—	—
<u>Cladonia spp. 10/</u>	6	12	<u>8/</u>	<u>8/</u>	—	—	—	—
<u>Nephroma arcticum</u>	1	2	<u>8/</u>	<u>8/</u>	—	—	—	—
<u>Peltigera aphthosa</u>	1	2	<u>8/</u>	<u>8/</u>	—	—	—	—
<u>Peltigera spp. 11/</u>	4	10	<u>8/</u>	<u>8/</u>	—	—	—	—
Litter components:								
Charred material	97	6	79	13	—	—	—	—
Leaves and twigs	98	7	17	17	—	—	—	—
Dead wood and fallen logs	98	5	4	3	—	—	—	—

1/ Number of stands sampled: 19; age: mean 2 years after fire (standard deviation 2); number of species found: mean 22 (standard deviation 5); depth of organic layer: mean 15 cm (standard deviation 7); depth of active thaw zone: mean 90 cm (standard deviation 39).

2/ Only species with a frequency of at least 30 percent in at least 1 stand are listed in tables 22-27. Not all of those species occur in every stage of succession; all are listed for each stage, however, to enhance comparison of their development.

3/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

4/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

5/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

6/ D.b.h. is the diameter of a tree at breast height. The values given are for trees 2.5 cm in d.b.h. or larger and are based on the equation: D.b.h. = Σ (mean d.b.h. values for a species in a stand) \div total number of stands sampled.

7/ Numbers in parentheses indicate the number of trees that originated before the fire.

8/ Less than 0.5 percent.

9/ Includes *Lycopodium clavatum*.

10/ Includes *Cladonia amaurocraea*, *C. alpestris*, and *Cladonia* spp.

11/ Includes *Peltigera canina*.

Table 24—Quantitative description of the tall shrub-sapling stage of plant succession on mesic black spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/

Quantitative description of the tall shrub-sapling stage								
Species and litter component 2/	Frequency 3/		Cover 4/		Density 5/		D.b.h. 6/	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
----- Percent -----				Stems/ha		Centimeters		
Tree layer:								
<u>Betula papyrifera</u> —								
Mature trees	2	5	—	—	1	2	3.8	1.4
Saplings	16	33	—	—	76	247	1.2	0.6
Seedlings	17	23	—	—	1,262	2,017	—	—
<u>Picea glauca</u> —								
Mature trees	7/ (3)	(9)	—	—	(1)	(2)	(11.8)	(4.8)
Saplings	6	16	—	—	2	5	1.2	0.6
Seedlings	14	30	—	—	1,631	3,606	—	—
<u>Picea mariana</u> —								
Mature trees	(8)	(20)	—	—	(2)	(5)	(8.6)	(3.9)
Saplings	8	18	—	—	4	7	1.5	0.6
Seedlings	40	40	—	—	12,881	29,251	—	—
<u>Populus tremuloides</u> —								
Mature trees	(5)	(22)	—	—	(43)	(195)	(5.2)	(0)
Saplings	15	34	—	—	1,377	5,930	0.9	0.4
Seedlings	27	36	—	—	6,012	18,131	—	—
Tall shrub layer:								
<u>Alnus crispa</u>	3	6	—	—	387	1,055	—	—
<u>Alnus tenuifolia</u>	1	4	—	—	310	1,418	—	—
<u>Betula glandulosa</u>	10	15	—	—	2,262	4,317	—	—
<u>Rosa acicularis</u>	33	24	—	—	2,952	3,320	—	—
<u>Rubus idaeus</u>	3	8	—	—	66	200	—	—
<u>Salix alaxensis</u>	1	2	—	—	25	85	—	—
<u>Salix arbusculoides</u>	11	24	—	—	1,804	5,351	—	—
<u>Salix bebbiana</u>	25	35	—	—	6,280	12,243	—	—
<u>Salix glauca</u>	9	23	—	—	1,458	5,453	—	—
<u>Salix planifolia</u>								
ssp. <u>pulchra</u>	8	14	—	—	1,905	5,864	—	—
<u>Salix scouleriana</u>	8	14	—	—	1,857	4,148	—	—
Other <u>Salix</u> spp.	14	29	—	—	1,530	3,809	—	—
Low shrub layer:								
<u>Empetrum nigrum</u>	2	9	8/	8/	—	—	—	—
<u>Ledum decumbens</u>	1	3	8/	1	—	—	—	—
<u>Ledum groenlandicum</u>	39	34	6	9	—	—	—	—
<u>Vaccinium oxycoccus</u>	8/	1	8/	8/	—	—	—	—
<u>Vaccinium uliginosum</u>	40	30	5	6	—	—	—	—
<u>Vaccinium vitis-idaea</u>	39	33	3	4	—	—	—	—
Herb layer:								
<u>Calamagrostis</u> spp.	57	28	5	6	—	—	—	—
<u>Cornus canadensis</u>	23	24	2	3	—	—	—	—
<u>Epilobium angustifolium</u>	63	33	3	8/	—	—	—	—
<u>Equisetum arvense</u>	9	35	1	3	—	—	—	—
<u>Equisetum scirpoides</u>	23	32	2	3	—	—	—	—
<u>Equisetum sylvaticum</u>	13	26	2	5	—	—	—	—
<u>Geocaulon lividum</u>	1	4	8/	8/	—	—	—	—
<u>Lycopodium annotinum</u> 9/	0	0	0	0	—	—	—	—
<u>Mertensia paniculata</u>	8	16	1	2	—	—	—	—
<u>Petasites frigidus</u>	5	12	8/	8/	—	—	—	—
<u>Rubus chamaemorus</u>	7	15	8/	2	—	—	—	—

See footnotes at end of table.

Table 24—Quantitative description of the tall shrub-sapling stage of plant succession on mesic black spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/ (continued)

Species and litter component <u>2/</u>	Quantitative description of the tall shrub-sapling							
	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Mosses:								
<u>Aulacomnium palustre</u>	19	32	2	5	—	—	—	—
<u>Aulacomnium turgidum</u>	8	22	2	8	—	—	—	—
<u>Ceratodon purpureus</u>	68	34	22	24	—	—	—	—
<u>Dicranum spp.</u>	2	5	8/	8/	—	—	—	—
<u>Drepanocladus uncinatus</u>	1	3	8/	8/	—	—	—	—
<u>Hylocomium splendens</u>	2	5	8/	8/	—	—	—	—
<u>Marchantia polymorpha</u>	12	21	2	4	—	—	—	—
<u>Pleurozium schreberi</u>	6	12	8/	1	—	—	—	—
<u>Polytrichum spp.</u>	52	35	8	15	—	—	—	—
<u>Sphagnum spp.</u>	1	4	8/	1	—	—	—	—
Unidentified moss	5	12	1	1	—	—	—	—
Lichens:								
<u>Cetraria cucullata</u>	0	0	0	0	—	—	—	—
<u>Cetraria islandica</u>	0	0	0	0	—	—	—	—
<u>Cladina arbuscula</u>	0	0	0	0	—	—	—	—
<u>Cladina rangiferina</u>	1	1	8/	8/	—	—	—	—
<u>Cladonia spp. 10/</u>	7	16	8/	1	—	—	—	—
<u>Nephroma arcticum</u>	0	0	0	0	—	—	—	—
<u>Peltigera aphthosa</u>	9	20	1	1	—	—	—	—
<u>Peltigera spp. 11/</u>	22	29	2	3	—	—	—	—
Litter components:								
Charred material	50	41	20	29	—	—	—	—
Leaves and twigs	97	12	48	25	—	—	—	—
Dead wood and fallen logs	76	25	6	3	—	—	—	—

1/ Number of stands sampled: 21; age: mean 10 years after fire (standard deviation 6); number of species found: mean 26 (standard deviation 11); depth of organic layer: mean 10 cm (standard deviation 4); depth of active thaw zone: mean 83 cm (standard deviation 21).

2/ Only species with a frequency of at least 30 percent in at least 1 stand are listed in tables 22-27. Not all of those species occur in every stage of succession; all are listed for each stage, however, to enhance comparison of their development.

3/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) - total number of stands sampled. Values have been rounded to the nearest whole number.

4/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) - total number of stands sampled. Values have been rounded to the nearest whole number.

5/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) - total number of stands sampled. Values have been rounded to the nearest whole number.

6/ D.b.h. is the diameter of a tree at breast height. The values given are for trees 2.5 cm in d.b.h. or larger and are based on the equation: D.b.h. = Σ (mean d.b.h. values for a species in a stand) - total number of stands sampled.

7/ Numbers in parentheses indicate the number of trees that originated before the fire.

8/ Less than 0.5 percent.

9/ Includes Lycopodium clavatum.

10/ Includes Cladonia amaurocraea, C. alpestris, and Cladina spp.

11/ Includes Peltigera canina.

Table 25—Quantitative description of the dense tree stage of plant succession on mesic black spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/

Quantitative description of the dense tree stage								
Species and litter component <u>2/</u>	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
----- Percent -----					Stems/ha		Centimeters	
Tree layer:								
<u>Betula papyrifera</u> —								
Mature trees	11	26	—	—	39	62	6.4	2.5
Saplings	8	20	—	—	4	8	1.9	0.4
Seedlings	1	3	—	—	42	97	—	—
<u>Picea glauca</u> —								
Mature trees	3	5	—	—	30	46	6.2	2.6
Saplings	6	9	—	—	22	67	1.5	0.6
Seedlings	<u>7/</u>	1	—	—	21	72	—	—
<u>Picea mariana</u> —								
Mature trees	86	26	—	—	2,163	1,408	5.4	0.7
Saplings	83	32	—	—	1,652	1,182	1.6	0.3
Seedlings	77	33	—	—	11,708	9,430	—	—
<u>Populus tremuloides</u> —								
Mature trees	17	33	—	—	358	736	8.1	0.4
Saplings	1	1	—	—	1	1	1.8	0.2
Seedlings	3	6	—	—	240	534	—	—
Tall shrub layer:								
<u>Alnus crispa</u>	8	15	—	—	822	1,773	—	—
<u>Alnus tenuifolia</u>	0	0	—	—	0	0	—	—
<u>Betula glandulosa</u>	16	30	—	—	2,750	4,979	—	—
<u>Rosa acicularis</u>	21	21	—	—	1,698	2,013	—	—
<u>Rubus idaeus</u>	0	0	—	—	0	0	—	—
<u>Salix alaxensis</u>	1	3	—	—	21	72	—	—
<u>Salix arbusculoides</u>	0	0	—	—	0	0	—	—
<u>Salix bebbiana</u>	2	4	—	—	42	111	—	—
<u>Salix glauca</u>	0	0	—	—	0	0	—	—
<u>Salix planifolia</u>								
ssp. <u>pulchra</u>	5	12	—	—	292	752	—	—
<u>Salix scouleriana</u>	3	7	—	—	458	1,255	—	—
Other <u>Salix</u> spp.	5	11	—	—	448	1,055	—	—
Low shrub layer:								
<u>Empetrum nigrum</u>	12	28	1	1	—	—	—	—
<u>Ledum decumbens</u>	18	30	1	3	—	—	—	—
<u>Ledum groenlandicum</u>	68	32	6	4	—	—	—	—
<u>Vaccinium oxycoccus</u>	6	14	<u>7/</u>	1	—	—	—	—
<u>Vaccinium uliginosum</u>	65	36	8	8	—	—	—	—
<u>Vaccinium vitis-idaea</u>	96	8	15	4	—	—	—	—
Herb layer:								
<u>Calamagrostis</u> spp.	50	38	1	1	—	—	—	—
<u>Cornus canadensis</u>	13	19	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Epilobium angustifolium</u>	4	12	<u>7/</u>	1	—	—	—	—
<u>Equisetum arvense</u>	25	34	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Equisetum scirpoides</u>	6	12	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Equisetum sylvaticum</u>	11	25	<u>7/</u>	1	—	—	—	—
<u>Geocaulon lividum</u>	28	30	1	2	—	—	—	—
<u>Lycopodium annotinum</u> <u>8/</u>	11	8	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Mertensia paniculata</u>	0	0	0	0	—	—	—	—
<u>Petasites frigidus</u>	8	13	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Rubus chamaemorus</u>	22	33	1	2	—	—	—	—

See footnotes at end of table.

Table 25—Quantitative description of the dense tree stage of plant succession on mesic black spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/ (continued)

Species and litter component <u>2/</u>	Quantitative description of the dense tree stage							
	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Mosses:								
<u>Aulacomnium palustre</u>	17	26	2	5	—	—	—	—
<u>Aulacomnium turgidum</u>	2	6	7/	7/	—	—	—	—
<u>Ceratodon purpureus</u>	2	3	1	7/	—	—	—	—
<u>Dicranum spp.</u>	40	21	1	1	—	—	—	—
<u>Drepanocladus uncinatus</u>	14	23	7/	1	—	—	—	—
<u>Hylocomium splendens</u>	45	26	10	8	—	—	—	—
<u>Marchantia polymorpha</u>	0	0	0	0	—	—	—	—
<u>Pleurozium schreberi</u>	90	10	36	19	—	—	—	—
<u>Polytrichum spp.</u>	64	20	4	5	—	—	—	—
<u>Sphagnum spp.</u>	19	28	6	12	—	—	—	—
<u>Unidentified moss</u>	11	14	7/	1	—	—	—	—
Lichens:								
<u>Cetraria cucullata</u>	6	13	7/	7/	—	—	—	—
<u>Cetraria islandica</u>	19	29	7/	1	—	—	—	—
<u>Cladina arbuscula</u>	16	28	1	3	—	—	—	—
<u>Cladina rangiferina</u>	46	25	4	4	—	—	—	—
<u>Cladonia spp. 9/</u>	56	24	3	3	—	—	—	—
<u>Nephroma arcticum</u>	13	14	1	2	—	—	—	—
<u>Peltigera aphthosa</u>	31	34	1	2	—	—	—	—
<u>Peltigera spp. 10/</u>	45	26	4	1	—	—	—	—
Litter components:								
Charred material	0	0	0	0	—	—	—	—
Leaves and twigs	100	1	23	24	—	—	—	—
Dead wood and fallen logs	80	22	6	3	—	—	—	—

1/ Number of stands sampled: 12; age: mean 48 years after fire (standard deviation 9); number of species found: mean 33 (standard deviation 3); depth of organic layer: mean 17 cm (standard deviation 4); depth of active thaw zone: mean 82 cm (standard deviation 41).

2/ Only species with a frequency of at least 30 percent in at least 1 stand are listed in tables 22–27. Not all of those species occur in every stage of succession; all are listed for each stage, however, to enhance comparison of their development.

3/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

4/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

5/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

6/ D.b.h. is the diameter of a tree at breast height. The values given are for trees 2.5 cm in d.b.h. or larger and are based on the equation: D.b.h. = Σ (mean d.b.h. values for a species in a stand) \div total number of stands sampled.

7/ Less than 0.5 percent.

8/ Includes *Lycopodium clavatum*.

9/ Includes *Cladonia amaurocraea*, *C. alpestris*, and *Cladina* spp.

10/ Includes *Peltigera canina*.

Table 26—Quantitative description of the mixed hardwood-spruce stage of plant succession on mesic black spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/

Quantitative description of the mixed hardwood-spruce stage								
Species and litter component 2/	Frequency 3/		Cover 4/		Density 5/		D.b.h. 6/	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Tree layer:								
<u>Betula papyrifera</u> —								
Mature trees	19	23	—	—	129	129	11.9	4.2
Saplings	8	11	—	—	4	9	1.7	0.4
Seedlings	1	2	—	—	68	130	—	—
<u>Picea glauca</u> —								
Mature trees	6	8	—	—	49	87	10.7	4.4
Saplings	8	11	—	—	5	9	1.6	0.4
Seedlings	7/	2	—	—	11	38	—	—
<u>Picea mariana</u> —								
Mature trees	85	20	—	—	1,550	1,183	7.3	1.5
Saplings	92	9	—	—	417	718	1.5	0.2
Seedlings	68	22	—	—	9,295	6,765	—	—
<u>Populus tremuloides</u> —								
Mature trees	30	43	—	—	470	678	15.6	4.6
Saplings	3	8	—	—	4	12	1.4	0.2
Seedlings	10	19	—	—	750	1,548	—	—
Tall shrub layer:								
<u>Alnus crispa</u>	15	22	—	—	1,557	2,456	—	—
<u>Alnus tenuifolia</u>	0	0	—	—	0	0	—	—
<u>Betula glandulosa</u>	0	0	—	—	0	0	—	—
<u>Rosa acicularis</u>	41	36	—	—	2,125	2,052	—	—
<u>Rubus idaeus</u>	0	0	—	—	0	0	—	—
<u>Salix alaxensis</u>	0	0	—	—	0	0	—	—
<u>Salix arbusculoides</u>	7/	2	—	—	11	38	—	—
<u>Salix bebbiana</u>	12	22	—	—	682	1,336	—	—
<u>Salix glauca</u>	7/	2	—	—	23	75	—	—
<u>Salix planifolia</u>								
ssp. <u>pulchra</u>	0	0	—	—	0	0	—	—
<u>Salix scouleriana</u>	4	8	—	—	295	725	—	—
Other <u>Salix</u> spp.	1	4	—	—	125	414	—	—
Low shrub layer:								
<u>Empetrum nigrum</u>	7	11	7/	7/	—	—	—	—
<u>Ledum decumbens</u>	1	3	7/	7/	—	—	—	—
<u>Ledum groenlandicum</u>	35	32	2	4	—	—	—	—
<u>Vaccinium oxycoccus</u>	0	0	0	0	—	—	—	—
<u>Vaccinium uliginosum</u>	59	30	5	6	—	—	—	—
<u>Vaccinium vitis-idaea</u>	87	15	8	6	—	—	—	—
Herb layer:								
<u>Calamagrostis</u> spp.	56	27	2	2	—	—	—	—
<u>Cornus canadensis</u>	55	35	2	3	—	—	—	—
<u>Epilobium angustifolium</u>	7	10	7/	7/	—	—	—	—
<u>Equisetum arvense</u>	13	30	1	2	—	—	—	—
<u>Equisetum scirpoides</u>	4	8	7/	7/	—	—	—	—
<u>Equisetum sylvaticum</u>	5	13	7/	7/	—	—	—	—
<u>Geocaulon lividum</u>	23	32	1	1	—	—	—	—
<u>Lycopodium annotinum</u> 8/	8	12	7/	7/	—	—	—	—
<u>Mertensia paniculata</u>	7	10	7/	7/	—	—	—	—
<u>Petasites frigidus</u>	1	3	7/	7/	—	—	—	—
<u>Rubus chamaemorus</u>	3	11	7/	7/	—	—	—	—

See footnotes at end of table.

Table 26—Quantitative description of the mixed hardwood-spruce stage of plant succession on mesic black spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/ (continued)

Quantitative description of the mixed hardwood-spruce stage								
Species and litter component <u>2/</u>	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Mosses:								
<u>Aulacomnium palustre</u>	2	3	<u>7/</u>	1	—	—	—	—
<u>Aulacomnium turgidum</u>	1	3	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Ceratodon purpureus</u>	1	3	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Dicranum spp.</u>	23	25	1	2	—	—	—	—
<u>Drepanocladus uncinatus</u>	14	22	<u>7/</u>	1	—	—	—	—
<u>Hylocomium splendens</u>	60	27	<u>23</u>	29	—	—	—	—
<u>Marchantia polymorpha</u>	0	0	0	0	—	—	—	—
<u>Pleurozium schreberi</u>	61	32	23	25	—	—	—	—
<u>Polytrichum spp.</u>	34	33	1	1	—	—	—	—
<u>Sphagnum spp.</u>	2	8	<u>7/</u>	1	—	—	—	—
Unidentified moss	13	17	<u>7/</u>	<u>7/</u>	—	—	—	—
Lichens:								
<u>Cetraria cucullata</u>	0	0	0	0	—	—	—	—
<u>Cetraria islandica</u>	8	24	<u>7/</u>	1	—	—	—	—
<u>Cladina arbuscula</u>	8	26	1	2	—	—	—	—
<u>Cladina rangiferina</u>	13	15	<u>7/</u>	1	—	—	—	—
<u>Cladonia spp. 9/</u>	25	23	1	2	—	—	—	—
<u>Nephroma arcticum</u>	15	27	1	2	—	—	—	—
<u>Peltigera aphthosa</u>	13	24	<u>7/</u>	1	—	—	—	—
<u>Peltigera spp. 10/</u>	23	30	2	2	—	—	—	—
Litter components:								
Charred material	1	2	1	2	—	—	—	—
Leaves and twigs	100	0	46	34	—	—	—	—
Dead wood and fallen logs	74	30	5	3	—	—	—	—

1/ Number of stands sampled: 11; age: mean 70 years after fire (standard deviation 26); number of species found: mean 31 (standard deviation 4); depth of organic layer: mean 14 cm (standard deviation 3); depth of active thaw zone: mean 57 cm (standard deviation 25).

2/ Only species with a frequency of at least 30 percent in at least 1 stand are listed in tables 22-27. Not all of those species occur in every stage of succession; all are listed for each stage, however, to enhance comparison of their development.

3/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

4/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

5/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

6/ D.b.h. is the diameter of a tree at breast height. The values given are for trees 2.5 cm in d.b.h. or larger and are based on the equation: D.b.h. = Σ (mean d.b.h. values for a species in a stand) \div total number of stands sampled.

7/ Less than 0.5 percent.

8/ Includes *Lycopodium clavatum*.

9/ Includes *Cladonia amaurocraea*, *C. alpestris*, and *Cladina* spp.

10/ Includes *Peltigera canina*.

Table 27—Quantitative description of the spruce stage of plant succession on mesic black spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/

Quantitative description of the spruce stage								
Species and litter component 2/	Frequency 3/		Cover 4/		Density 5/		D.b.h. 6/	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- Percent -----				Stems/ha		Centimeters	
Tree layer:								
<u>Betula papyrifera</u> —								
Mature trees	6	8	—	—	26	30	17.0	11.7
Saplings	0	0	—	—	0	0	—	—
Seedlings	1	2	—	—	31	62	—	—
<u>Picea glauca</u> —								
Mature trees	9	14	—	—	88	128	17.8	7.5
Saplings	0	0	—	—	0	0	—	—
Seedlings	0	0	—	—	0	0	—	—
<u>Picea mariana</u> —								
Mature trees	99	2	—	—	1,680	473	15.2	1.2
Saplings	52	55	—	—	225	300	1.6	0.4
Seedlings	40	37	—	—	4,688	4,942	—	—
<u>Populus tremuloides</u> —								
Mature trees	0	0	—	—	0	0	—	—
Saplings	0	0	—	—	0	0	—	—
Seedlings	0	0	—	—	0	0	—	—
Tall shrub layer:								
<u>Alnus crispa</u>	34	17	—	—	5,062	3,686	—	—
<u>Alnus tenuifolia</u>	0	0	—	—	0	0	—	—
<u>Betula glandulosa</u>	0	0	—	—	0	0	—	—
<u>Rosa acicularis</u>	39	48	—	—	2,656	3,161	—	—
<u>Rubus idaeus</u>	0	0	—	—	0	0	—	—
<u>Salix alaxensis</u>	0	0	—	—	0	0	—	—
<u>Salix arbusculoides</u>	1	2	—	—	31	62	—	—
<u>Salix bebbiana</u>	0	0	—	—	0	0	—	—
<u>Salix glauca</u>	1	2	—	—	156	312	—	—
<u>Salix planifolia</u>								
ssp. <u>pulchra</u>	0	0	—	—	0	0	—	—
<u>Salix scouleriana</u>	0	0	—	—	0	0	—	—
Other <u>Salix</u> spp.	1	2	—	—	31	62	—	—
Low shrub layer:								
<u>Empetrum nigrum</u>	14	24	1	2	—	—	—	—
<u>Ledum decumbens</u>	16	32	2	3	—	—	—	—
<u>Ledum groenlandicum</u>	58	45	8	8	—	—	—	—
<u>Vaccinium oxycoccus</u>	9	18	7/	1	—	—	—	—
<u>Vaccinium uliginosum</u>	42	40	2	3	—	—	—	—
<u>Vaccinium vitis-idaea</u>	100	0	16	10	—	—	—	—
Herb layer:								
<u>Calamagrostis</u> spp.	78	26	4	4	—	—	—	—
<u>Cornus canadensis</u>	2	5	7/	7/	—	—	—	—
<u>Epilobium angustifolium</u>	0	0	0	0	—	—	—	—
<u>Equisetum arvense</u>	6	10	7/	7/	—	—	—	—
<u>Equisetum scirpoides</u>	21	42	1	2	—	—	—	—
<u>Equisetum sylvaticum</u>	49	54	4	5	—	—	—	—
<u>Geocaulon lividum</u>	70	16	4	2	—	—	—	—
<u>Lycopodium annotinum</u> 8/	8	12	7/	1	—	—	—	—
<u>Mertensia paniculata</u>	0	0	0	0	—	—	—	—
<u>Petasites frigidus</u>	0	0	0	0	—	—	—	—
<u>Rubus chamaemorus</u>	24	44	2	4	—	—	—	—

See footnotes at end of table.

Table 27—Quantitative description of the spruce stage of plant succession on mesic black spruce sites in the taiga of interior Alaska, by dominant plant species and litter component 1/ (continued)

Species and litter component <u>2/</u>	Quantitative description of the spruce stage							
	Frequency <u>3/</u>		Cover <u>4/</u>		Density <u>5/</u>		D.b.h. <u>6/</u>	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
	----- <u>Percent</u> -----				<u>Stems/ha</u>		<u>Centimeters</u>	
Mosses:								
<u>Aulacomnium palustre</u>	9	12	1	2	—	—	—	—
<u>Aulacomnium turgidum</u>	0	0	0	0	—	—	—	—
<u>Ceratodon purpureus</u>	0	0	0	0	—	—	—	—
<u>Dicranum spp.</u>	18	17	1	<u>7/</u>	—	—	—	—
<u>Drepanocladus uncinatus</u>	15	17	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Hylocomium splendens</u>	85	13	34	22	—	—	—	—
<u>Marchantia polymorpha</u>	0	0	0	0	—	—	—	—
<u>Pleurozium schreberi</u>	74	40	34	26	—	—	—	—
<u>Polytrichum spp.</u>	26	34	2	3	—	—	—	—
<u>Sphagnum spp.</u>	19	38	5	10	—	—	—	—
Unidentified moss	9	10	<u>7/</u>	<u>7/</u>	—	—	—	—
Lichens:								
<u>Cetraria cucullata</u>	0	0	0	0	—	—	—	—
<u>Cetraria islandica</u>	6	12	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Cladina arbuscula</u>	15	3	1	1	—	—	—	—
<u>Cladina rangiferina</u>	14	28	1	2	—	—	—	—
<u>Cladonia spp. 9/</u>	16	6	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Nephroma arcticum</u>	0	0	0	0	—	—	—	—
<u>Peltigera aphthosa</u>	2	3	<u>7/</u>	<u>7/</u>	—	—	—	—
<u>Peltigera spp. 10/</u>	16	26	<u>7/</u>	1	—	—	—	—
Litter components:								
Charred material	0	0	0	0	—	—	—	—
Leaves and twigs	100	0	18	10	—	—	—	—
Dead wood and fallen logs	90	9	6	4	—	—	—	—

1/ Number of stands sampled: 4; age: mean 121 years after fire (standard deviation 56); number of species found: mean 31 (standard deviation 11); depth of organic layer: mean 16 cm (standard deviation 5); depth of active thaw zone: mean 59 cm (standard deviation 31).

2/ Only species with a frequency of at least 30 percent in at least 1 stand are listed in tables 22-27. Not all of those species occur in every stage of succession; all are listed for each stage, however, to enhance comparison of their development.

3/ The percent of plots in which a given species occurs. It is based on the equation: Frequency = Σ (mean stand frequency value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

4/ The percent of area shaded by the canopy of a given species or litter component. It is based on the equation: Cover = Σ (mean stand cover value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

5/ The computed or counted number of stems occurring in a given area. It is based on the equation: Density = Σ (mean stand density value for a species) \div total number of stands sampled. Values have been rounded to the nearest whole number.

6/ D.b.h. is the diameter of a tree at breast height. The values given are for trees 2.5 cm in d.b.h. or larger and are based on the equation: D.b.h. = Σ (mean d.b.h. values for a species in a stand) \div total number of stands sampled.

7/ Less than 0.5 percent.

8/ Includes *Lycopodium clavatum*.

9/ Includes *Cladonia amaurocraea*, *C. alpestris*, and *Cladina* spp.

10/ Includes *Peltigera canina*.

Table 28—Summary of the quantitative descriptions of the 6 stages of plant succession on mesic black spruce sites in the talga of Interior Alaska 1/

Item	Newly burned stage		Moss-herb stage		Tall shrub-sapling stage		Dense tree stage		Mixed hardwood-spruce stage		Spruce stage	
	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation	Mean	Standard deviation
Stand age, years	0.1	0	2	2	10	6	48	9	70	26	121	56
Plant species found, number 2/	12	3	22	5	26	11	33	3	31	4	31	11
Depth of organic layer, centimeters	11	8	15	7	10	4	17	4	14	3	16	5
Depth of active thaw zone, centimeters	49	9	90	39	83	21	82	41	57	25	59	31
Number of stems per hectare												
Density: 3/ 4/												
Tree layer—												
Mature trees	0	0	5/ (48)	(154)	47	194	2,595	1,267	2,211	984	1,800	539
Saplings	0	0	13	23	1,461	5,915	1,682	1,204	430	718	225	300
Seedlings	0	0	29,210	43,669	22,589	32,098	12,062	9,077	10,125	6,501	4,719	4,972
Tall shrub layer—												
Salix spp.	1,042	1,181	1,392	1,948	14,859	15,733	1,261	1,460	1,136	1,414	218	438
Other tall shrubs	625	760	3,362	6,059	5,977	5,226	5,396	4,624	3,920	2,737	7,750	5,070
Percent												
Cover: 4/ 6/												
Low shrubs	1	1	10	9	15	15	32	14	17	8	29	22
Herbs	2	1	11	8	18	14	5	3	6	3	16	6
Mosses	7/	7/	14	11	37	30	60	23	50	34	80	18
Lichens	7/	7/	1	1	3	3	18	10	7	10	2	2
Litter components	106	2	100	14	74	26	29	26	51	32	23	11

1/ Number of stands sampled: newly burned, 3; moss-herb, 19; tall shrub-sapling, 21; dense tree, 12; mixed hardwood-spruce, 11; spruce, 4.

2/ Also includes the 3 stages of tree development: mature, sapling, and seedling. When present, each stage of a species is counted as 1.

3/ The computed or counted number of stems occurring in a given area.

4/ Totals may be off because of rounding and because data listed were only for the species occurring most frequently.

5/ Numbers in parentheses indicate the number of trees that originated before the fire.

6/ The percent of area shaded by the canopy of a given plant layer or litter component.

7/ Less than 0.5 percent.

Patterns of Change on Mesic Black Spruce Sites

As with white spruce sites, each developmental stage on black spruce sites can be described individually, yet together they form patterns that change through time. Figure 24 illustrates the changes; each graph in the figure is limited to one stratum.

Trees begin as seedlings of black spruce or as seedlings and suckers of quaking aspen or paper birch. Young trees appear in the newly burned stage, are present in greatest numbers during the moss-herb stage, and decrease in number thereafter (fig. 24A). A small number of seedlings and suckers become saplings and trees; most of them die. Seedlings of black spruce are more numerous than those of other species throughout black spruce succession (fig. 24B). The hardwood seedlings develop faster than black spruce. Most saplings in the tall shrub-sapling stage are quaking aspen and paper birch, whereas most saplings in the dense tree stage are black spruce (fig. 24C). Black spruce trees and saplings usually dominate from the dense tree stage on (fig. 24D). Hardwood species occur during the dense tree and mixed hardwood-spruce stages but rapidly decrease in numbers thereafter.

Willows appear in the newly burned stage, increase slowly to their greatest numbers in the tall shrub-sapling stage, and decrease thereafter (fig. 24E). All willows follow this general trend. Bebb willow was the most extensive in the stands studied, but Scouler, grayleaf, littletree, and diamondleaf willows were also important.

The non-willow tall shrubs show four trends (fig. 24F). (1) American green alder, appearing in small quantities in the newly burned stage, increases steadily in numbers to become the most extensive non-willow tall shrub in the spruce stage. (2) Prickly rose appears in the newly burned stage, reaches greatest density

during the tall shrub-sapling stage, then decreases slightly and maintains that level. (3) Resin birch appears in the newly burned stage and increases slowly to greatest density in the dense tree stage. Thereafter in this study, it was found only near timberline. (4) American red raspberry is present in small quantities in the young successional stages but is not found after the tree-dominated stages develop.

Low shrubs appear in the newly burned stages, develop slowly but steadily through the tall shrub-sapling stage, and provide the most cover during the dense tree and spruce stages (fig. 24G). They appear to be less important in the mixed hardwood-spruce stage. All species tend to follow this trend, although Labrador-tea expands slightly faster than other species, and bog blueberry may decrease slightly during the spruce stage. Mountain-cranberry appears to be the most extensive low shrub in the tree-dominated stages.

Herb cover begins in the newly burned stages and increases to peak early in the tall shrub-sapling stage and again in the spruce stage (fig. 24H). Herb cover is less during the dense tree and mixed hardwood-spruce stages. This general pattern is the result of three overlapping trends: (1) species such as Geocaulon lividum and Lycopodium spp. appear early, increase slowly, and reach greatest cover in the spruce stage; (2) species such as fireweed and tall bluebell appear early, increase rapidly, develop greatest cover in the tall shrub-sapling stage, and decline thereafter; and (3) many species are present through all stages; of these, reedgrass, cloudberry, and woodland horsetail are the most common and extensive.

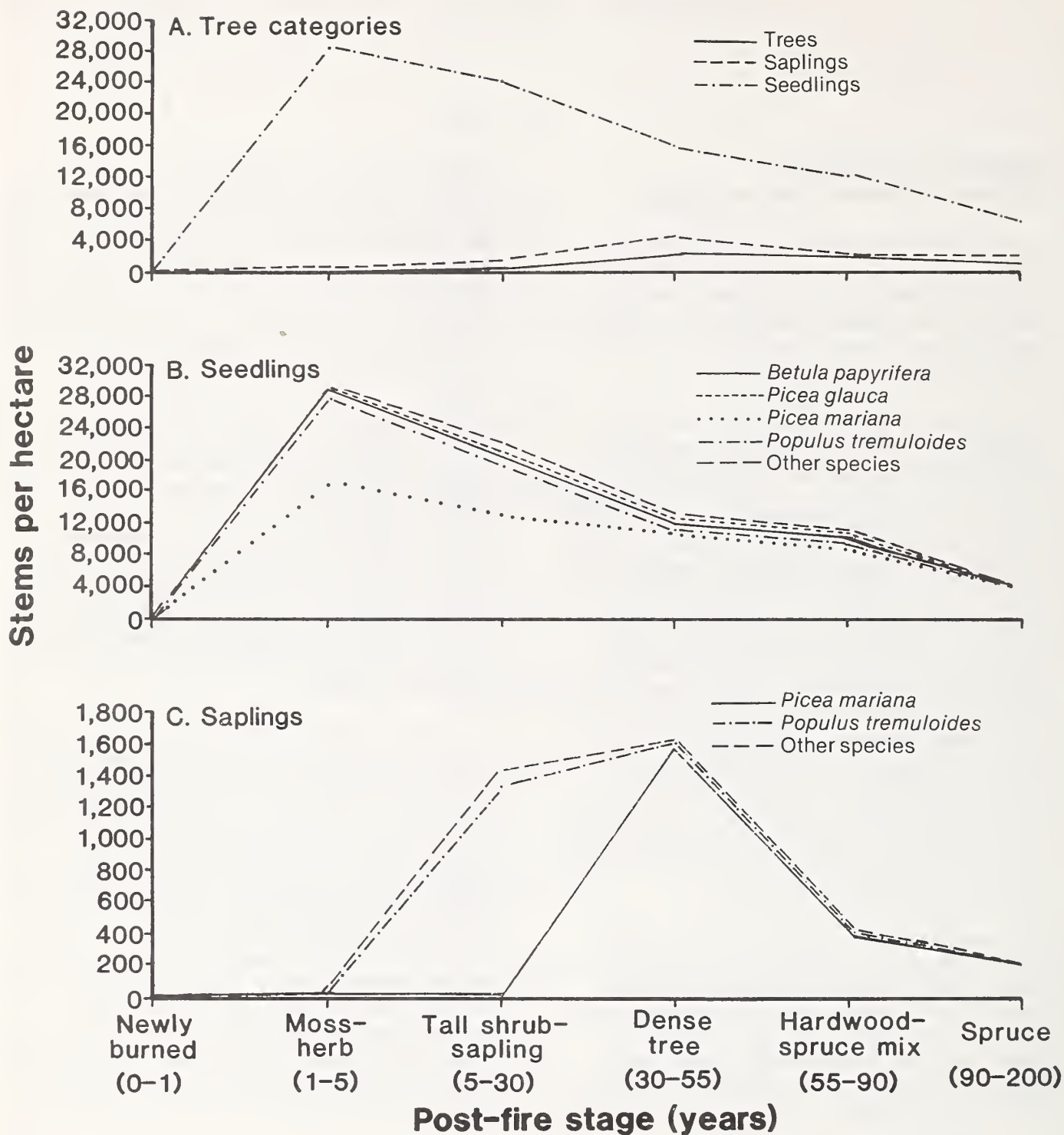


Figure 24.—Successional trends on black spruce sites. Shown are densities of A, tree categories; B, seedlings; C, saplings; D, trees; E, tall shrubs, willow; and F, tall shrubs, non-willow. Also shown are the covers of G, low shrubs; H, herbs; I, mosses and

liverworts; J, lichens; and K, litter. Other items shown are L, depth of organic layer; M, thickness of ground thaw zone; and N, number of species present. Each line represents the number occurring of that unit. Graphs with more than one line show cumulative totals.

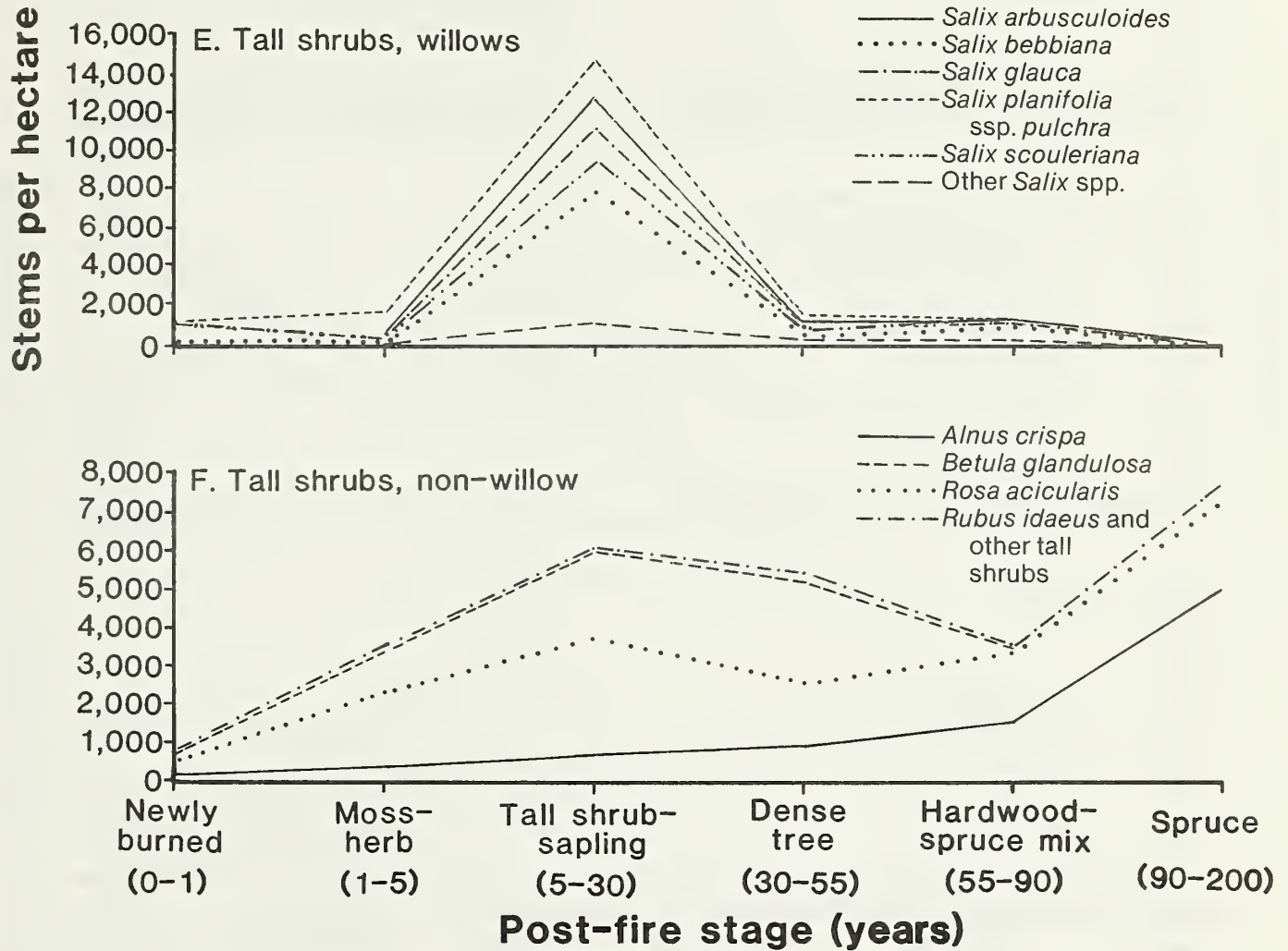


Figure 24.—(continued)

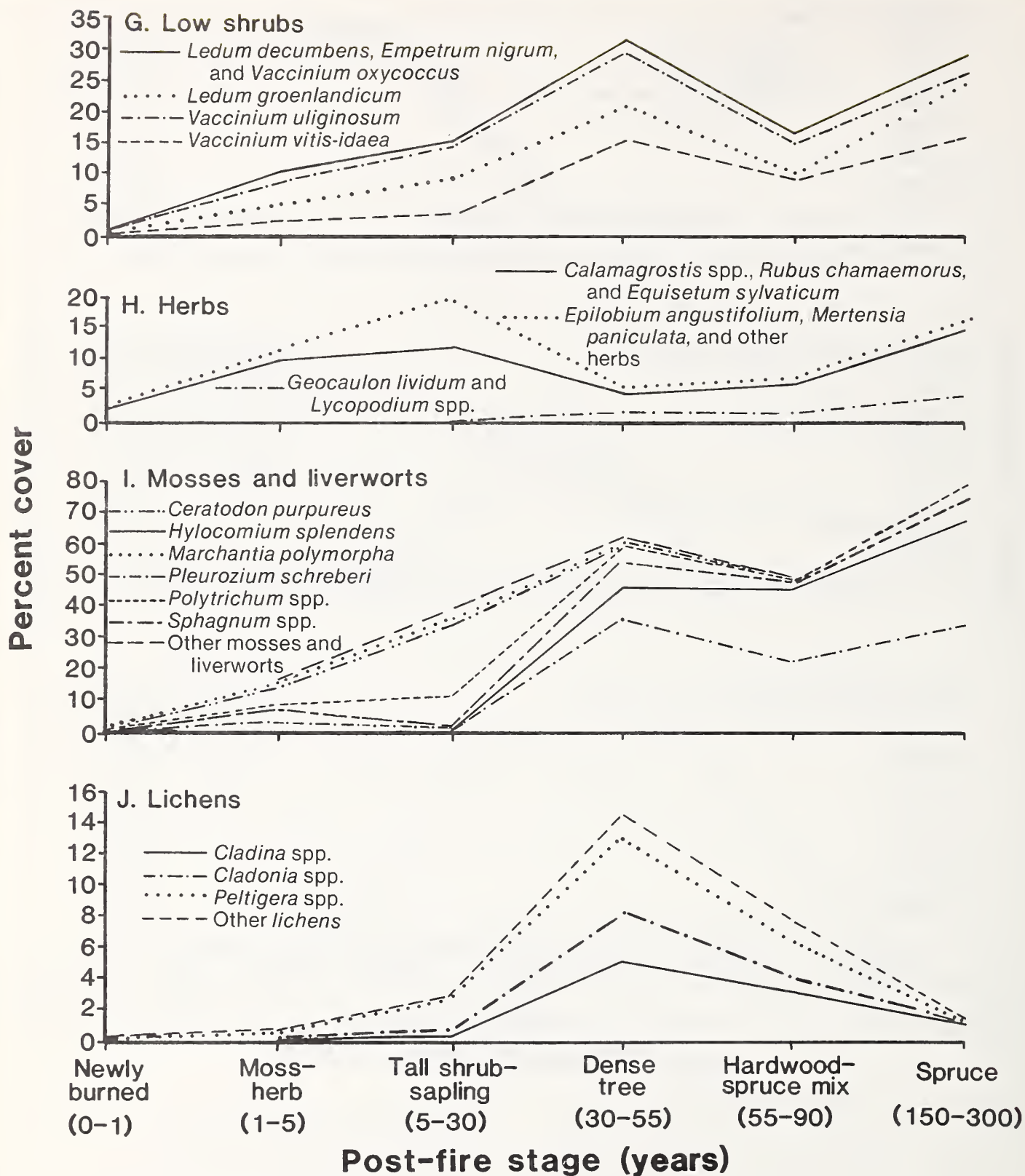


Figure 24.—(continued)

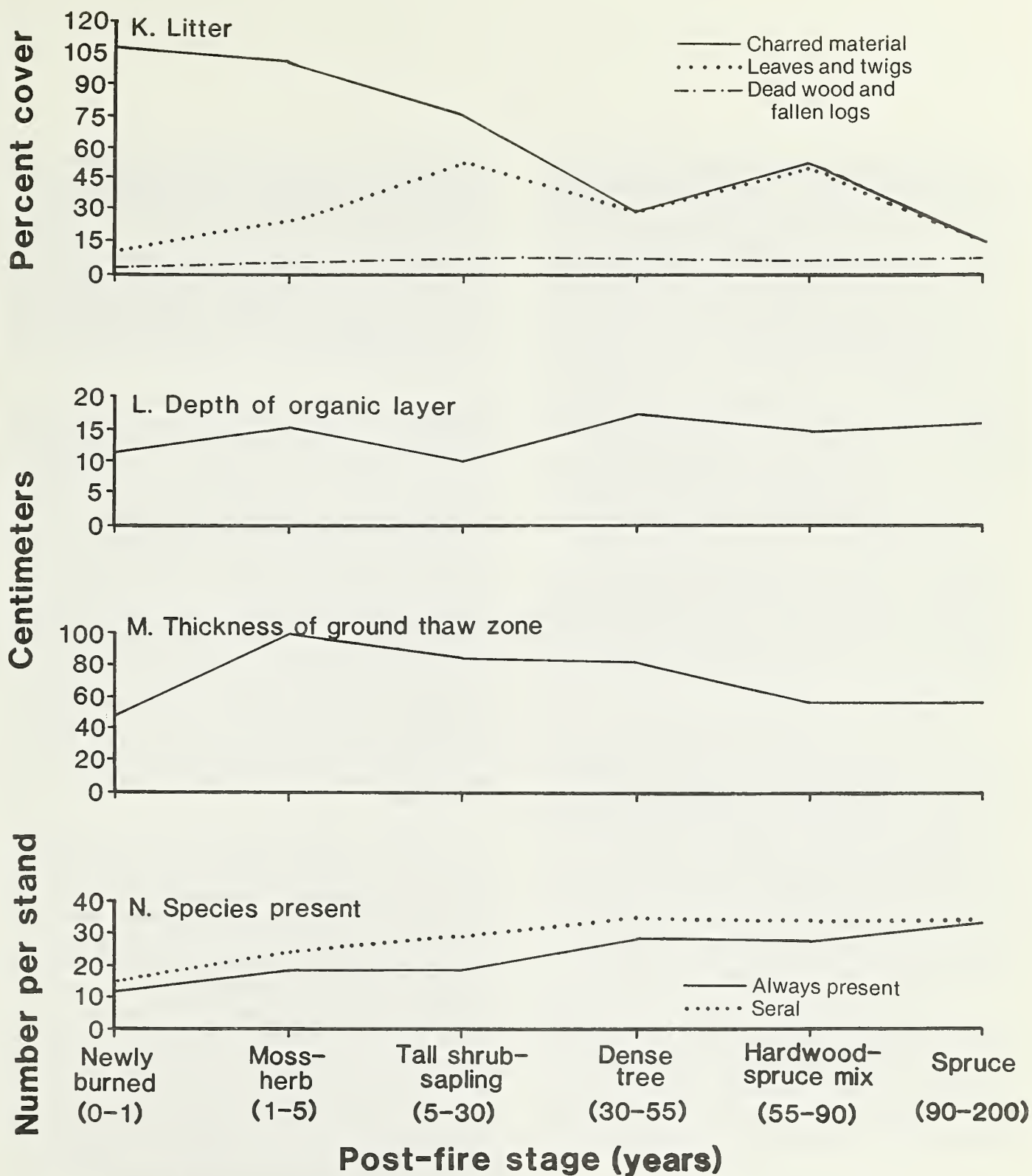


Figure 24.—(continued)

Mosses begin in the newly burned stage and increase almost steadily to cover the most area during the spruce stage (fig. 24I). This trend is reversed during the mixed hardwood-spruce stage, when mosses tend to be slightly less extensive beneath hardwoods. This pattern is the result of three overlapping trends. (1) Feathermoss and Sphagnum species appear sometime during the first three stages but increase simultaneously and suddenly with the emergence of black spruce trees. Pleurozium schreberi expands first and covers the most area in the dense tree stage. Hylocomium splendens expands next most rapidly and codominates the forest floor with Pleurozium schreberi thereafter. Sphagnum spp. increase more slowly and dominate only in the wetter sites. (2) Polytrichum spp. are always present but amounts vary. (3) Ceratodon purpureus and Marchantia polymorpha appear soon after fire, expand rapidly to cover the greatest area during the early tall shrub-sapling stage, and decline rapidly thereafter.

Ground lichens all follow one pattern (fig. 24J). They appear slowly and increase gradually to cover the greatest area during the dense tree stage, after which they slowly decline. Peltigera spp. are the first to appear, and they usually occur in the greatest amounts. Cladina spp. and Cladonia spp. account for most of the remaining lichen cover. On mesic sites in this study, only small quantities of lichens were found in stands representing the spruce stage of development.

Litter in the newly burned stage is composed mostly of charred surfaces (fig. 24K). With time, these surfaces disappear and most are covered by the end of the tall shrub-sapling stage. Deadfall litter increases as vegetation develops and is most abundant during the tall

shrub-sapling stage and again during the mixed hardwood-spruce stage, when deciduous and annual leaf fall is greatest. Exposed logs are always present on the forest floor. The area they cover increases gradually, levels off during the tall shrub-sapling stage, and stays fairly constant thereafter. Dead trees fall and become logs, old logs decay and are gradually covered by moss.

Beneath the forest floor, patterns of change also occur. Thickness of the organic layer and the thaw zone above permafrost change (figs. 24L and M). The organic layer is thinnest immediately after fire and increases with time. On the other hand, thickness of the thaw zone increases with time but only for a while. It then slowly decreases until it reaches equilibrium with the insulating vegetation layer above. Immediately after fire, the blackened and burned surfaces absorb radiant energy, raising soil temperatures and melting permafrost. This heatsink state continues until the surface becomes less black and vegetation, especially feathermoss, once again insulates the ground from solar heating. In time, the permafrost stops melting and may start reforming.

The number of plant species present changes with time (fig. 24N). Species are found immediately after fire. This number steadily increases, with the greatest number occurring during the dense tree stage; thereafter the number stabilizes or decreases slightly. Few species are seral; that is, present only in the younger stages of succession. Most species, once they appear, remain throughout succession but vary in importance. The following species, listed in approximate order of increasing duration, come the closest to being seral: Marchantia polymorpha, Ceratodon purpureus, fireweed, American red raspberry, most willows, quaking aspen, and paper birch.

The result of succession on mesic black spruce sites is a somewhat open stand of black spruce trees under which are found American green alder, mountain-cranberry, Labrador-tea, bog blueberry, Geocaulon lividum, reedgrass, Pleurozium schreberi, Hylocomium splendens, and Sphagnum spp. in varying amounts. The feathermosses, Pleurozium schreberi and Hylocomium splendens, dominate the forest floor which is usually underlain by permafrost.

The six mature forest community types that occur on black spruce sites can now be seen in perspective. Each is the most mature phase of its respective community type. This study suggests, however, that in the absence of fire, types 7 through 10 (see table 2), or all the black spruce found on mesic sites that have been discussed, will become type 9, the Picea mariana/Vaccinium uliginosum-Ledum groenlandicum/Pleurozium schreberi community type. Since fire burns most areas before they reach 100 years in age, and since most older stands show at least some evidence of earlier burning, type 9 may represent the vegetation best able to withstand fire and not necessarily the theoretical end point of succession.

Two types, 11 and 12 (see table 2), do not reflect mesic black spruce sites so were not used in the discussion of succession. They may be important, however, because of what they tell us about lichen cover. Type 11, the Picea mariana-Picea glauca/Betula glandulosa/lichen community type, occurs near timberline. The question is whether its extensive lichen cover is due to its proximity to tundra, where lichens may be extensive, or to the presence of two dominant age classes. The latter possibility suggests that the most recent fire, which occurred about 55 years ago, burned a 55- to 100-year-old spruce/lichen stand. At least some of the lichens survived the fire and have since expanded to produce what occurs today.

Type 12, the Picea mariana/Sphagnum spp.-Cladina community type, occurs on valley bottoms in a muskeg-bog setting. Here trees, lichens, and Sphagnum spp. occur on areas raised above the water table by developing ice lenses or by islands of bedrock. In these areas, lichens are found in 60- and 130-year-old stands. At least under these conditions, it appears lichens do not die out as succession advances.

Comparison of Patterns of Change

Succession on white spruce and on black spruce sites is both similar and dissimilar. It may be useful to compare the two processes.

1. Successional series of both white spruce and mesic black spruce may pass through six developmental stages: newly burned, moss-herb, tall shrub-sapling, dense tree, hardwood (or hardwood-spruce), and spruce. The length of each stage varies, however, depending on the growth rate and development of the taller growing species present. The first three stages last 20-25 years on white spruce sites and 30-35 years on black spruce sites, or the time it takes the trees to overtop the lower growing vegetation. The hardwood stage on white spruce sites lasts 50-100 years and on black spruce sites 30-50 years, but may be completely absent. In theory, the spruce stage on both sites can last indefinitely.

2. Revegetation for both successional series starts from shoots, seeds, spores, etc., but these propagules are not equally available on all sites. Vegetative and in situ seed reproduction immediately after fire tends to be greater on black spruce sites than on white spruce sites.

3. Most species occur on both white spruce and black spruce sites; quaking aspen, paper birch, prickly rose, mountain-cranberry, bunchberry, reedgrass, fireweed, Pleurozium schreberi, Hylocomium splendens, Ceratodon purpureus, and Marchantia polymorpha are some. No species are restricted to one site type but some show a preference. White spruce, high bushcranberry, twin-flower, and field horsetail are good indicators of warm, well-drained sites. Black spruce, Sphagnum spp., bog blueberry, cloudberry, and woodland horsetail are indicators of moister and cooler, but still mesic sites.

4. Some species in both successional series develop their greatest numbers and/or cover in the early stages and decline or disappear in later stages. Marchantia polymorpha, Ceratodon purpureus, fireweed, and American red raspberry follow this trend. In terms of density only, quaking aspen and paper birch fall in this group.

5. Other species in both series develop their greatest numbers and/or cover in the intermediate stages and decline or disappear thereafter. Bebb, grayleaf, and Scouler willows as well as Peltigera spp. are important in the tall shrub stage. Cladonia spp. and Cladina spp. are important in the dense tree stage. And quaking aspen and paper birch may be important in the dense tree and hardwood stages. The lichen species are more extensive on black spruce sites and the hardwood species on white spruce sites.

6. Still other species attain their greatest densities and cover in the spruce stage of both successional series. American green alder, twin-flower, Geocaulon lividum, and white spruce (trees only) develop slowly and continuously after they first appear. Pleurozium schreberi, Hylocomium splendens, and Sphagnum spp. expand very little during the first three stages, expand explosively during the dense tree stage, and hold their own or continue to expand thereafter.

7. Some species fluctuate but are always present. Prickly rose and reedgrass follow this pattern on all sites, field horsetail and high bushcranberry on white spruce sites, and woodland horsetail and cloudberry on black spruce sites.

8. Fire can terminate succession at any point. Fire on black spruce sites is common, and most sites burn before stands are 100 years old. Fire on white spruce sites is less common, and many white spruce stands are more than 100 years old.

9. Today's landscape is the product of successional changes. Each forest-dominated stand is in one of the three tree-dominated stages. Mature types 1, 2, 3, 7, and 8 (see table 2) all contain hardwood species, and stands typifying them are examples of the hardwood stage of development. Types 4, 5, and 9-12 (see table 2) are primarily spruce-dominated. Stands of these types are in the spruce stage of development.

Metric Equivalents

$$^{\circ}\text{C} = 5/9 (^{\circ}\text{F} - 32)$$

$$1 \text{ centimeter (cm)} = 0.39 \text{ inch}$$

$$1 \text{ meter (m)} = 3.28 \text{ feet}$$

$$1 \text{ hectare (ha)} = 2.47 \text{ acres}$$

$$1 \text{ cubic meter per hectare (m}^3\text{/ha)} \\ = 14.29 \text{ cubic feet per acre}$$

$$1 \text{ kilometer (km)} = 0.62 \text{ mile}$$

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Appendix

Scientific and Common Names of Plants 8/

TREES:

Betula papyrifera Marsh. var. humilis
(Reg.) Fern. & Raup^{9/ 10/}

Paper birch

Larix laricina (Du Roi) K. Koch

Tamarack, Alaska larch

Picea glauca (Moench) Voss^{9/ 10/}

White spruce

Picea mariana (Mill.) B.S.P.^{9/ 10/}

Black spruce

Populus balsamifera L.^{9/ 10/}

Balsam poplar

Populus tremuloides Michx.^{9/ 10/}

Quaking aspen

TALL SHRUBS:

Alnus crispa (Ait.) Pursh^{9/}

American green alder

Alnus tenuifolia Nutt.

Thinleaf alder

Betula glandulosa Michx.^{9/}

Resin birch, bog birch

Betula glandulosa X B. papyrifera

Hybrid birch

Oplopanax horridus (Sm.) Miq.^{9/}

Devilsclub

Rosa acicularis Lindl.^{9/}

Prickly rose

Rubus idaeus L. var. strigosus

American red raspberry

(Michx.) Maxim.

Salix alaxensis (Anderss.) Cov.

Feltleaf willow

Salix arbusculoides Anderss.

Littletree willow

Salix bebbiana Sarg.^{9/}

Bebb willow

Salix glauca L.^{9/}

Grayleaf willow

8/ Sources for names: trees, tall shrubs, and low shrubs—Viereck and Little (1972) and Kelsey and Dayton (1942); herbs—Hultén (1968), Welsh (1974), and Kelsey and Dayton (1942); mosses—Worley and Watuski (1970); and lichens—Hale and Culberson (1970).

9/ Species used in the reduced species list for the clustering analysis of stands.

10/ Seedlings, saplings, and mature trees were treated as separate entities in the cluster analysis.

Salix planifolia Pursh. ssp. pulchra

(Cham.) Argus^{9/}

Salix scouleriana Barratt^{9/}

Viburnum edule (Michx.) Raf.^{9/}

Diamondleaf willow

Scouler willow

High bushcranberry

LOW SHRUBS:

Arctostaphylos uva-ursi (L.) Spreng.

Betula nana L.^{9/}

Chamaedaphne calyculata (L.) Moench

Empetrum nigrum L.^{9/}

Ledum decumbens (Ait.) Small^{9/}

Ledum groenlandicum Oeder^{9/}

Linnaea borealis L.^{9/}

Ribes spp.

Spiraea beauverdiana Schneid.^{9/}

Vaccinium oxycoccus L.^{9/}

Vaccinium uliginosum L.^{9/}

Vaccinium vitis-idaea L.^{9/}

Bearberry

Dwarf arctic birch

Leatherleaf

Crowberry, black crowberry

Narrow-leaf Labrador-tea,

sprawling crystaltea ledum

Labrador-tea, Labradortea ledum

Twin-flower, American twinflower

Currant

Beauverd spirea

Bog cranberry, small cranberry

Bog blueberry, bog bilberry

Mountain-cranberry, cowberry

HERBS:

Calamagrostis canadensis (Michx.)

Beauv.^{9/}

Calamagrostis spp.^{9/}

Carex spp.

Cornus canadensis L.^{9/}

Dryopteris dilatata (Hoffm.) Gray^{9/}

Epilobium angustifolium L.^{9/}

Equisetum arvense L.^{9/}

Equisetum pratense Ehrh.

Equisetum scirpoides Michx.^{9/}

Bluejoint

Reedgrass

Sedge

Bunchberry, dwarf dogwood

Spinulose shield-fern, mountain

woodfern

Fireweed

Field horsetail, meadow horsetail

Meadow horsetail

Dwarf scouring-rush, sedgelike

horsetail

Equisetum sylvaticum L.^{9/}

Eriophorum vaginatum L.

Galium boreale L.

Galium triflorum Michx.

Geocaulon lividum (Richards.) Fern^{9/}

Lycopodium annotinum L.

Lycopodium clavatum L. ssp. monospachyon
(Grev. & Hook.) Sel.

Lycopodium complanatum L.^{9/}

Mertensia paniculata (Ait.) G. Don^{9/}

Moenringia lateriflora (L.) Frenzl^{9/}

Pedicularis labradorica Wirsing

Petasites frigidus (L.) Fries

Polygonum alaskanum (Small) Wright

Pyrola asarifolia Michx.

Pyrola chlorantha Sw.

Pyrola secunda L.

Rubus chamaemorus L.^{9/}

Streptopus amplexifolius (L.) DC.

Woodland horsetail, Sylvan horsetail

Tussock cottongrass, sheathed
cottensedge

Northern bedstraw

Sweet-scented bedstraw

(No common name)

Stiff clubmoss

Running clubmoss

Ground cedar

Tall bluebell, panicle bluebell

Blunt-leaved sandwort

Labrador lousewort

Arctic sweet coltsfoot

Alaska wild rhubarb

Liverleaf wintergreen, alpine pyrola

Green pyrola

One-sided wintergreen sidebells
pyrola

Cloudberry

Clasping twisted-stalk, claspleaf
twistedstalk

MOSSES AND LIVERWORTS:

Aulacomnium palustre (Hedw.)

Schwaegr.^{9/}

(No common name)

Aulacomnium turgidum (Wahlenb.)

Schwaegr.

(No common name)

Ceratodon purpureus (Hedw.) Brid.^{9/}

(No common name)

Dicranum spp.

(No common name)

Drepanocladus uncinatus (Hedw.) Warnst.

(No common name)

Hylocomium splendens (Hedw.) B.S.G.^{9/}

Feathermoss

Marchantia polymorpha L.^{9/}

(No common name)

Pleurozium schreberi (Brid.) Mitt.^{9/}

Polytrichum spp.^{9/ 11/}

Ptilium crista-castrensis (Hedw.) De Not.

Rhytidiadelphus triquetrus (Hedw.)

Warnst.

Sphagnum spp.^{9/}

Feathermoss

(No common name)

Feathermoss

Feathermoss

(No common name)

LICHENS:

Cetraria cucullata (Bell.) Ach.^{9/}

Cetraria islandica (L.) Ach.^{9/}

Cetraria richardsonii Hook

Cladina arbuscula (Wallr.) Hale &

W. Culb. (= Cladonia sylvatica (L.)

Hoffm.)^{9/}

Cladina rangiferina (L.) Harm.

(= Cladonia rangiferina (L.) Web.)^{9/}

Cladonia gracilis (L.) Willd.

Cladonia spp.^{9/}

Nephroma arcticum (L.) Torss.^{9/}

Peltigera aphthosa (L.) Willd.

Peltigera canina (L.) Willd.^{9/}

Peltigera spp.^{9/}

(No common name)

(No common name)

(No common name)

Reindeer lichen

Reindeer lichen

(No common name)

(No common name)

(No common name)

(No common name)

(No common name)

(No common name)

^{11/}Includes three species: Polytrichum commune Hedw., P. juniperinum Hedw., and P. piliiferum Hedw.

Foote, M. Joan. Classification, description, and dynamics of plant communities after fire in the taiga of interior Alaska. Res. Pap. PNW-307. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1983. 108 p. One hundred thirty forest stands ranging in age from 1 month postfire to 200 years were sampled and described by successional series (white spruce and black spruce) and by developmental stage (newly burned, moss-herb, tall shrub-sapling, dense tree, hardwood, and spruce). Patterns of change in the two successional series are described. In addition, 12 mature forest communities are described in quantitative and qualitative terms.

Keywords: Communities (plant), classification (plant communities), fire (-plant ecology, taiga, Alaska (interior)).

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